HOW REWILDING IMPACTS ECOSYSTEM HEALTH IN A SEMI-ARID REGION

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ABSTRACT

Rewilding represents more than just the reintroduction of iconic charismatic species; it holds the potential to assist in reestablishing critical ecosystem functions, helping create dynamic, resilient, and self-sustaining ecosystems. Here I test the general idea that *the reintroduction of megafauna such as elephant, rhino, and buffalo will alter soil and vegetation characteristics as well as dung beetle assemblages via megafauna trampling and feeding behaviours, ultimately improving ecosystem health*. This was conducted in two different vegetation types, Montagu Shale Renosterveld and Western Klein Karoo. By examining these key indicators of ecosystem health, this research has revealed that the rewilded areas generally exhibit higher levels of dung beetle abundance (up to 3.7 times higher than livestock areas), improved soil dynamics (e.g. 11–12% lower bulk density), and greater vegetation productivity as shown by EVI trends. The study also investigated the potential of leveraging carbon credits as a means to fund restoration projects in semi-arid settings, but ultimately concluded that a more nuanced approach is likely needed in the form of biodiversity credits. Ultimately, this study provides tentative evidence that well-managed rewilding can indeed assist in restoring degraded landscapes. This, in turn, reaffirms the crucial role of nature-based solutions in biodiversity conservation and highlights the importance of positive land stewardship and management. These findings underscore the importance and viability of embracing rewilding as a legitimate method by which to protect and regenerate degraded landscapes. In addition, this study illustrates how the impact of rewilding is not uniform across ecosystem types by comparing findings between the two stated vegetation types. All these findings suggest that a more holistic approach is needed to evaluate and value rewilding initiatives, one which includes key ecological variables such as vegetation dynamics, various soil characteristics, and insect populations. By taking an interdisciplinary approach to conservation through combining rigorous ecological assessments with innovative financing mechanisms (such as biodiversity credits) in the future, it is more likely to capture the multifaceted benefits of rewilding and foster long-term ecosystem resilience. This comprehensive strategy is pivotal for transforming biodiversity conservation and ensuring robust ecological recovery across diverse landscapes, while increasing the likelihood of financial viability and sustainability of rewilding projects.

INTRODUCTION

1.1: Climate Change

The face of conservation has changed drastically over the years, particularly in the Global South (Green *et al*., 2015). From a pursuit which focused on the intrinsic value of nature, humanity has slowly moved towards a system which acknowledges the instrumental value of biodiversity and ecosystems (Justus *et al*., 2009; Mariki, 2016; (IPBES, 2019). With this realisation comes the acknowledgement that human beings are not only dependent on biodiversity, but also part of many natural systems. This is evident in the move towards ecosystem conservation, which acknowledges the importance of certain human activities to thriving ecosystems and ecosystem health (Cumming, 2016; Sangha *et al*., 2021). Thus, integrated approaches to conservation efforts, such as Community-based Natural Resource Management (CBNRM), are becoming more common worldwide (Gillson *et al*., 2019).

These advances in understanding are, nonetheless, underpinned largely by scientific evidence acquired in Northern Hemisphere conservation efforts. Furthermore, even when not, North-centric solutions are often applied to Global South conservation problems (Reidpath and Allotey, 2019). Often, this approach yields underwhelming results, as contexts differ so drastically. Region-specific research is necessary to successfully achieve positive outcomes with key conservation and climate-oriented efforts (Nguyen and Tran, 2019). Nowhere is this more evident than in the climate change mitigation- focused aspects of conservation, particularly where soils are involved (Biermann and Möller, 2019; Láng *et al*., 2016). Soils sustain roughly 60% of the world's total biodiversity (Anthony, Bender and van der Heijden, 2023), produce 98% of human calories and sequester around 80% of the total carbon stock in terrestrial ecosystems. In addition, soils support the potential solutions to many of our most pressing environmental issues, with food production and carbon storage being key examples (Anthony, Bender and van der Heijden, 2023; Robinson *et al.*, 2024). Presently, a 2°C increase in global temperatures relative to pre-industrial revolution temperatures, appears to be likely by 2100 without substantive mitigation efforts, with some projections suggesting that an increase >3°C is a possibility (Weber *et al*., 2018). While it has been shown that a change of 1.5°C will very likely cause severe negative socioeconomic impacts, particularly for emerging nations, the impact of a 3°C change will likely be orders of magnitude more damaging (Donnelly *et al*., 2017; Weber *et al*., 2018; Masson-Delmotte *et al*., 2019).

Despite this, the concentration of major greenhouse gases, particularly carbon dioxide (CO_2), is projected to increase until 2035 (and possibly beyond) and has done so since just after the Second

World War (Hofmann, Butler and Tans, 2009). Indeed, CO_2 levels have risen over 50% since preindustrial times, from an estimated 278ppm in 1750 to well above 420ppm in 2025. Alarmingly, this overall trend appears to be consistent across multiple high-impact greenhouse gases such as methane (CH_4), which experienced a 165% rise and nitrous oxide (NO_2) (Cubasch *et al*., 2019) (Masson-Delmotte *et al*., 2019).

In response to these alarming trends, governments worldwide- along with the UN- have introduced numerous climate change mitigation and adaptation policies and measures (Puppim De Oliveira, 2009; Khan and Roberts, 2013). Examples of these include the Convention on Climate change (COP 28), the UN Sustainable Development Goals (SDGs), and the Paris Agreement. Moreover, many nations have implemented their own climate change policies (Puppim De Oliveira, 2009). South Africa, for example, has approved a Low Emissions Development Strategy (LEDS), a National Climate Change Adaptation Strategy (NCCAS) and a carbon tax, all aimed at addressing some of the causes and impacts of climate change (Moyo, 2016). Unfortunately, these measures are slow to take effect and largely fall short of the mark (Moyo, 2016; Santos, Ferreira and Pedersen, 2022).

1.2: Nature-Based Solutions

Nature-based Solutions (NBS) offer the potential to partially, but effectively, address several insufficiencies extant in the climate change mitigation and adaptation strategies, at both a local and global level (Griscom *et al*., 2017; Bradfer-Lawrence *et al*., 2021). The purpose of NBS is to sustainably mitigate climate change without trade-offs for society, biodiversity, water quality and food security. Examples of this include green infrastructure, wetland restoration, habitat restoration and regenerative agriculture. Most forms of NBS are reliant on ecosystem functions and are strongly reliant on the conservation, restoration and effective management of ecosystems to maximise ecosystem output and natural capital development; a topic discussed in detail below (Kronenberg, 2016; Lafortezza *et al*., 2018). Of particular interest to the authors are Natural Climate Solutions (NCS), climate-specific NBS which seek to reduce greenhouse gas production and/or store carbon through improved land management, as well as habitat conservation and restoration. Specifically, the rehabilitation of rangelands, through rewilding, to increase ecosystem health and resilience for the ultimate purpose of carbon sequestration (Griscom *et al*., 2017). Notably, however, although attention on both NBS and NCS has grown significantly in recent times, neither are solutions to the climate change crises on their own (Seddon *et al*., 2020).

1.3: Rewilding

Rewilding is a novel and swiftly developing form of biodiversity stewardship which aims to regenerate degraded landscapes to establish an ecologically sound state, through the utilization of ecosystem functioning and processes such as trophic cascades and ecosystem engineers. While rewilding is similar to habitat restoration, with the terms often used interchangeably, there are key differences between the two. The focus of habitat restoration (restoration ecology) is to return an ecosystem to as close to a former benchmark state as possible. Rewilding, on the other hand, does not (du Toit and Pettorelli, 2019).

While definitions, specifics and approaches to rewilding vary considerably across the board (Schulte Te Bühne, Pettorelli and Hoffmann, 2022), rewilding generally takes a holistic and novel approach to landscape regeneration and conservation, emphasizing biodiversity and functionality rather than historical benchmarking (Navarro and Pereira, 2012; Perino *et al*., 2019). Furthermore, rewilding involves rejuvenating and regenerating degraded landscapes with the emphasis on current and future ecosystem function, and thus on ecosystem services (du Toit and Pettorelli, 2019). Ultimately, rewilding is an effort to address and provide a pragmatic response to the rapidly changing environmental factors associated with the Anthropocene (Atkinson *et al*., 2024).

Key principles of rewilding are ecosystem sustainability and self-regulation to reduce the need for costly managerial input and increase the likelihood of the establishment of a sound and resilient ecosystem. This outcome is highly desirable, given the extent of land degradation worldwide; the limited resources available to address the issue and the urgency with which these issues need to be addressed (Svenning *et al*., 2016; Fernández, Navarro and Pereira, 2017). Of particular importance to this study are functional and trophic rewilding approaches that make use of reintroducing extant and ecologically significant species- often Megafauna- to a degraded landscape. The aim of this approach is to rejuvenate trophic interaction and subsequent cascades in a top-down manner. This is intended to produce self-managing and functional biodiversity and ecosystems (Svenning *et al*., 2016; Guyton *et al*., 2020; Atkinson *et al*., 2024). Within the context of this study, the authors seek to achieve this outcome through the reintroduction of elephant (*Loxodonta africana*), buffalo (*Syncerus caffra*), black rhinoceros (*Diceros bicornis)* and African lion (*Pantherus leo*); all of which occurred historically in the study area. It is thought that the reintroduction of these species will restore ecosystem function through the movement, nutrient cycling and feeding habits of these ecosystem engineers (Berzaghi *et al*., 2019; Kalbitzer *et al*., 2019; Trepel *et al*., 2024) and ultimately restore ecosystem health and resilience.

1.4: Ecosystem Status

As stated above, many nature-based solutions are reliant on ecosystem functioning that support ecosystem services. While some ecosystem functions are resilient even under degraded and suboptimal settings, the greatest benefit is derived when these systems operate at their highest potential when ecosystems are as healthy, intact and functional as possible. It's at this optimised point where the derived ecosystem services are maximized (Griscom *et al*., 2017; van Den Bosch and Ode Sang, 2017; Lafortezza *et al*., 2018). Therefore, it is of particular importance to define and understand the benefits of healthy ecosystems.

Ecosystem health is defined by the system's sustainability and resilience, thus its ability to maintain structure and function, even when exposed to external stressors (Costanza, 2012; Costanza and Mageau, 1999). Thus, the healthier, more intact and more complete an ecosystem, the greater its ability to function and handle and adapt to change (Puettmann, 2014; Scarano, 2017; Watson *et al*., 2018). It's for this reason that ecosystem health is of such importance to natural climate solutions.

Land use has a significant impact on ecosystem function, including soil health, nutrient cycling, and biodiversity. Further, it has implications for climate change via sequestration of carbon into living biomass and particularly, soil organic carbon (SOC). With growing populations and thus demand for living space and food, the importance of land use efficiency continues to grow. This is as true for food production as it is for conservation, thus, the land sparing vs land sharing debate continues to be relevant (Smith, 2008; Ekroos *et al.*, 2016). Land sparing conserves biodiversity on protected areas but places relatively high pressure on the remaining land for agricultural production. Land sharing attempts to meet both agricultural conservation goals on the same land, with potential trade-offs for both activities unless properly managed. Further, it is in these landscapes where fragmentation becomes a concern (Selinske *et al.*, 2023).

However, habitat fragmentation is often misunderstood owing to its complexity. There are many factors which dictate the magnitude of the impact that fragmentation has on the ecosystem, ecosystem services and thus, biodiversity. By ensuring that matrix quality is high, connectivity is maintained and habitat segment size is appropriate, the impact of land sharing on biodiversity can be reduced (Ekroos *et al.*, 2016). Soil is a key aspect of biodiversity and matrix quality and can be used as an indicator of ecosystem health and a way to protect ecosystem resilience to change and disruption. Rewilding may form part of land restoration in cases of severe land degradation, (Bustamante *et al.*, 2023; Tälle *et al.*, 2023) but ideally systematic assessment of ecosystem health is required with potential replenishment of missing components such as plant and animal populations (Simba *et al* 2023).

Land degradation, which can occur through 17 different processes (GLASOD classification) (Oldeman *et al*., 1991), is of particular concern world over, with almost half of all land experiencing degradation to a greater or lesser extent (IPBES, 2019). In the Global South, 26% of the total global costs of land degradation come from sub-Saharan Africa alone. This translates to ecosystems that are operating at suboptimal levels, hindering ecosystem health, ecosystem function and ultimately, ecosystem services. In addition, it leaves these areas vulnerable to further degradation and damage due to external stressors such as rapidly changing climatic conditions. Others, still, have been wiped out almost completely (Nkonya *et al*., 2016; Navarro *et al*., 2017; Prăvălie, 2021; Bai and Cotrufo, 2022). Therefore, preventing land degradation is vital to the global population, not only from an economic perspective but an environmental perspective too. A feat that can be accomplished, at least in part, through rewilding (Navarro *et al*., 2017).

Trophic levels and cascades

Trophic cascades are powerful emergent ecological phenomena. On land, the concept acknowledges the importance of soil as the base trophic level, which supports primary producers, particularly plant communities. As such there are both top-down (predator driven) and bottom-up (soil or other lower trophic levels) effects known as trophic cascades (Atkins *et al.*, 2019). For example, predators may influence herbivore numbers and behaviour, which in turn influence plant communities and the soil and its fauna. Recently, research has shown that similar process occurs with non-predatory Megafauna (Guyton *et al.*, 2020; Svenning, 2020).

A disturbance at the primary level can have profound implications for higher trophic levels, particularly when the ecosystem in question is sensitive to change. This is particularly relevant to ecosystems that historically have high levels of biodiversity that has been degraded over time due to substantial and sustained disturbances. The reintroduction of Megafauna and ecosystem engineers can play a pivotal role in restoring ecosystem health at a primary level by reactivating essential ecological processes (Guyton *et al.*, 2020). Large animals, such as elephant, rhino and buffalo, influence vegetation communities and structure, soil dynamics, and nutrient cycling. This is achieved through browsing, trampling, and seed dispersal, which in turn impacts soil structure and fertility. Their actions help prevent the dominance of certain plant species, maintaining- or boosting- biodiversity and promoting a balanced, resilient ecosystem (Kalbitzer *et al.*, 2019; Gordon *et al.*, 2023).

Ecosystem engineers, such as dung beetles and other soil fauna, further enhance soil health by aerating the soil through burrowing, which improves water infiltration and nutrient distribution. This soil disturbance positively impacts microbial communities and primary producers (such as plants), creating a healthier base trophic level (Hajji *et al.*, 2024). In landscapes where reintroductions have occurred, these processes help reverse the degradation caused by historical disturbances such as livestock and crop agriculture. By restoring these natural interactions, ecosystems regain resilience, supporting a more stable and interconnected food web from the soil up. This is of course desirable, particularly with the increasing threat of more severe climate change (Egoh *et al.*, 2021; Arya, 2023; Hajji *et al.*, 2024).

From a conservation perspective, soil contains most of the world's biodiversity and is (arguably) the foundation of all terrestrial ecosystems. It supports a vast array of organisms, including fungi, bacteria, earthworms, and insects, all of which play critical roles in nutrient cycling, organic matter decomposition, and plant growth (Anthony, Bender and van der Heijden, 2023; Robinson *et al.*, 2024). While research has been conducted on African soils, particularly in South Africa, much soil research is concentrated in the Global North. As a result, global practices and standards for soil health, fertility, and management practices are largely based on the characteristics of these temperate-region soils. This reliance on Northern models creates a significant gap when addressing the diverse and unique properties of South African soils, which span a range of biomes and environmental conditions (Fey, 2010; Rakotonarivo and Andriamihaja, 2023). This is concerning, especially for a country like South Africa, which contains such immense soil diversity, from nutrient-rich grasslands to arid, sandy soils. It can be argued, then, that context-specific research is required for local soils to inform accurate norms, standards, and ultimately both policy and management decisions (Fey, 2010). Without such localized understanding, conservation and agricultural efforts may fail to maximize soil health and ecosystem resilience.

Traditionally, soil and soil health are divided into three main characteristic categories: Biological, physical, and chemical. Biological characteristics include microorganism communities, soil fauna, and organic matter. Examples of physical characteristics include texture, structure, and porosity, while chemical composition focuses on nutrient content, pH, and salinity, among others. Much is known about physical characteristics of soils, and this aspect has thus been the primary focus when evaluating soil health (Karlen, Andrews and Doran, 2001). However, there is increasing recognition of the importance of biological characteristics and their role in enhancing overall soil health, both in conservation and agricultural settings. This is particularly true of fungal and bacterial communities, which contribute to soil fertility, disease suppression, and ecosystem resilience (Raghavendra *et al.*, 2020; FAO 2020). By integrating biological, physical, and chemical factors into soil health assessments, more holistic and effective management practices can be developed to support sustainable ecosystems.

1.5: Measures of Ecosystem Status

To understand the impact that reintroduced ecosystem engineers have had on the local ecosystems, several proxies can be used (Gerlach *et al*., 2013; Nichols *et al*., 2008), e.g., soil health, vegetation and soil fauna indices.

1.5.1 Dung beetles

To understand, assess, and predict the impact of anthropogenic activity, a deep understanding of biodiversity and ecological functions is required. It is within this context that biological indicators and ecosystem services have value (Gerlach *et al*., 2013; Nichols *et al*., 2008). Dung beetles, as both biological indicators and ecosystem engineers, are a noteworthy group. They contribute greatly to many ecosystem functions, providing an array of ecosystem services, and because of their sensitivity to change, make for effective biological indicators of ecosystem health (Doube, 2018; Gerlach *et al*., 2013).

Contributing to ecosystem health and regulation in both adult and larval stages, these beetles perform key roles through the manipulation of faeces during feeding. This process drives important ecosystem functions such as nutrient cycling, parasite suppression, seed dispersal, trophic regulation, pollination, and bioturbation (the dispersal of nutrients through the soil column). Notably, these functions underpin many of the ecosystem services on which human well-being depends (Nichols *et al*., 2008; Prather *et al*., 2013). The value of their presence is further magnified in areas where they once occurred but are now locally extinct. While dung decomposition relies on various other decomposers, dung beetles remain a key element (O’Hea *et al*., 2010). This was illustrated in the 1960s CSIRO case study in Australia, where exotic bovid dung remained unaltered on the soil surface for extended periods, rendering it unavailable as a nutrient source and contributing to fly outbreaks. The issue was later resolved by introducing non-native dung beetles, many from South Africa, that facilitated decomposition (Nichols *et al*., 2008). Additionally, dung beetle activity increases soil aeration, as well as the soil’s ability to absorb and retain water through the deposition of organic matter. This is particularly important in semi-arid zones, especially in an African context, where the likelihood of bioturbation by other means is reduced. In these ways, dung beetles significantly shape habitats and influence habitat dynamics (Nichols *et al*., 2008; Tind Nielsen, 2007).

Dung beetles' effectiveness as biological indicators stems partly from their being well-studied, relatively large, and easy to survey, but also from their high sensitivity to habitat and environmental changes, including shifts in dung type and availability (Gerlach *et al*., 2013; McGeoch *et al*., 2011; van Rensburg *et al*., 1999). They respond strongly to land use changes, particularly urban and agricultural activities such as ploughing, biocide application, and livestock grazing, and abiotic factors like altitude and temperature (Englmeier *et al*., 2022). The majority of dung beetle research has been conducted in tropical and semi-tropical regions, with many studies focused on the Americas. This geographic bias may leave gaps in our understanding of their roles in drier regions, such as parts of southern Africa (Correa *et al*., 2022; Mora-Aguilar *et al*., 2023).

A clear grasp of the relationship between ecological functions and biodiversity is essential to accurately assess the environmental consequences of human activities (McGeoch *et al*., 2002). Because dung beetles feed on faeces in both adult and larval stages, they initiate vital ecological functions like nutrient cycling, bioturbation, secondary seed dispersal, and parasite suppression. These processes, in turn, support ecosystem services such as soil fertilization, enhanced plant growth, and biological pest control (Kalbitzer *et al*., 2019; Hajji *et al*., 2024). While their role in pollination and trophic regulation may be limited, their sensitivity to habitat modification and changes in dung availability means that these critical functions can be disrupted if ecosystems are altered or degraded (Tind Nielsen, 2007; Kalbitzer *et al*., 2019; Asha *et al*., 2021). By tracking changes in dung beetle populations, one can gain valuable insights into overall ecosystem health and better guide conservation efforts that maintain these essential services. Moreover, further research spanning diverse regions is crucial to fully understand and safeguard the important roles dung beetles play worldwide (Nichols *et al*., 2009; Milotić *et al*., 2017). Biological indicators like dung beetles encompass multiple functional groups, making them particularly useful for assessing environmental changes (Gerlach *et al*., 2013). The use of ecological, environmental, and biodiversity indicators is key to understanding habitat state and the impacts of both biotic and abiotic shifts (McGeoch *et al*., 2002). Although indicator taxa can sometimes be considered unreliable for broad-scale biodiversity assessments, they are invaluable for identifying specific ecological characteristics and local-scale changes (Janion-Scheepers *et al*., 2016; McGeoch *et al*., 2002).

While a number of generalist dung beetle species respond well to various dung types (Mora-Aguilar *et al*., 2023), including human dung, some species show a distinct preference for faeces from particular local fauna (Whipple and Hoback, 2012). One study found that, although dung diversity was beneficial overall, elephant dung was especially favoured and played the most critical role in supporting local dung beetle diversity (Pryke *et al*., 2022). This niche differentiation suggests an evolutionary link between certain dung beetles and their preferred dung producers (Englmeier *et al*., 2022). Consequently, having a variety of herbivores, differing in size and feeding behaviour, positively influences dung beetle diversity and, by extension, promotes ecosystem self-regulation and health (Pryke *et al*., 2022, 2016). This supports the rewilding argument, raising the question of what other biodiversity and ecosystem functions might return to degraded landscapes if key Megafauna ecosystem engineers were reintroduced.

1.5.2 Nutrient Cycling

Nutrient cycling is a key force driving the health of soil and ecosystems. Nutrient cycling is defined as the cyclic process of nutrient movement from organisms to the environment and back, which is key to sustained ecosystem function (Marschner and Rengel, 2007; Klumpp, 2021). Most organisms play a part in nutrient cycling, with some playing pivotal roles in the distribution and processing of nutrients throughout their respective ecosystems (Kooch *et al.*, 2022; Tessler *et al.*, 2023). This movement and processing of nutrients, making nutrients available to primary consumers, sustains soil health and ultimately ecosystem functionality. Megafauna, particularly ecosystem engineers like elephants and large herbivores, facilitate nutrient distribution through activities like foraging, trampling, and dung deposition. The rewilding concept therefore recognises the key role of Megafauna in nutrient cycling (du Toit and Pettorelli, 2019; Egoh *et al.*, 2021; Arya, 2023).

With the reintroduction of these key species, ecosystems are encouraged to return to their natural state, improving nutrient dynamics and making them more resilient to future climatic change. Key ecosystem variables are once again included, leading to potential long-term repair of ecosystems and their services (Guyton *et al.*, 2020; Svenning, 2020). Soils, soil organisms, and plant communities re-establish as secondary, tertiary, and quaternary consumers return. In many ecosystems, this results in improved soil nutrient levels and cycling, particularly in nitrogen, phosphorus, and carbon, promoting healthier and more balanced ecosystems (Luo *et al.*, 2020; Brezonik and Arnold, 2022).

1.6: Ecosystem Services and Carbon Sequestration

As a key primary provider of ecosystem services such as carbon storage, water purification and nutrient cycling, the importance of soil and soil conservation is evident (Keesstra *et al.*, 2018; Southern Illinois University, USA *et al.*, 2018). Under the right conditions, soil also serves as a filter for potentially harmful contaminants, playing a key role in clean and healthy ecosystems. As such, soil is a key component in functional natural systems (Pereira *et al.*, 2018). Soils support not only microorganism communities, but primary producers, that makes soil the key base layer to numerous complex ecosystems (Kihara *et al.*, 2020; Telo Da Gama, 2023) .

From a climate change perspective, the carbon storage potential of soils requires further explanation. Climate change solutions can generally be divided into either adaptation or mitigation strategies. Carbon management falls into both categories. From a mitigation perspective, carbon capture looks to reduce climatic CO_2 levels, thereby lowering greenhouse gas presence in the atmosphere and ultimately resulting in some climate change mitigation. In terms of adaptation, we have changed, and continue to change, the way in which we manage our soils and ecosystems. The move away from tillage and heavy synthetic fertiliser and biocide use, towards no-till, regenerative agriculture, are relevant examples (Lal, Negassa and Lorenz, 2015; Steinhoff-Knopp, Kuhn and Burkhard, 2021; Robinson *et al.*, 2024).

As estimated by the Global Carbon Budget, soils (2 400 gigatons) hold as much carbon as the atmosphere (860 gigatons) and vegetation (650 gigatons) combined, making them one of the most critical terrestrial carbon sinks globally (Friedlingstein *et al.*, 2019). Aboveground biomass in the form of vegetation is indeed important, however, this form of carbon sink is highly vulnerable and variable in nature. Vegetation is inherently sensitive to degradation and disturbances such as fire, land-use change, and climate disturbances. While still susceptible to degradation and land use change, belowground carbon storage in soil, in contrast, is significantly more stable and long-lasting. However, it must be remembered that both forms of carbon sink are deeply linked (Tian *et al.*, 2023; Keller *et al.*, 2024).

Carbon, in all its various forms, is vital to soil health and central to many major conservation and climate change goals. Soil Organic Carbon (SOC) refers to the amount of carbon found and stored in organic matter, largely originating from animal residues and decaying plant material, more than 50% of which is found in the top 1 m of the soil profile (Lal, Negassa and Lorenz, 2015). Organic matter acts not only as a store of carbon but also as a source for key nutrients for plants, including nitrogen, sulphur, and phosphorus (Anikwe and Ife, 2023). It also plays an important structural role in the soil, contributing to aeration and water retention. Biome-appropriate levels of SOC support diverse microbial communities, which are essential for decomposing organic matter, cycling nutrients, and maintaining soil structure. This microbial activity is fundamental to overall soil health and ecosystem productivity (Gleixner *et al.*, 2002; Luo *et al.*, 2020; Batool, Cihacek and Alghamdi, 2024). Soils rich in organic matter (and thus organic carbon) exhibit improved water infiltration and water-holding capacity, making them more resilient to changing climatic conditions such as droughts and floods (Naorem, 2022; Telo Da Gama, 2023). This is a result of relatively lower bulk densities and an increased number of hydrophilic particles in the soil. These properties are particularly crucial for maintaining productive landscapes and protecting ecosystems in the face of climate variability (Keesstra *et al.*, 2018; Pereira *et al.*, 2018; Mattila and Vihanto, 2024).

In contrast, Soil Inorganic Carbon (SIC) refers to the accumulation of carbon in mineral forms, usually carbonates. While SIC is not directly involved in nutrient cycling, it plays a crucial role in regulating soil pH and buffering acidity, making it essential for the stability of many ecosystems, particularly arid and semi-arid regions. SIC can also contribute to long-term carbon storage, locking carbon into stable forms for centuries (Srivastava *et al.*, 2012; Batool, Cihacek and Alghamdi, 2024). SIC levels can also be negatively impacted by adverse effects, namely soil degradation, leading to a reduction in sequestration potential (Steinhoff-Knopp, Kuhn and Burkhard, 2021)

While both SOC and SIC contribute to removing carbon from the atmosphere, it is generally SOC and not SIC that can be manipulated and is thus more relevant for carbon credits in terrestrial ecosystems. As a concept, carbon credits incentivize conservation practices that promote carbon sequestration, thereby helping offset greenhouse gas emissions (Taguchi, 2023). Beyond carbon storage, increasing soil carbon provides additional co-benefits such as improved soil fertility, greater vegetation growth, and enhanced biodiversity as mentioned. These multifunctional benefits makes soil carbon sequestration a valuable tool for both conservation and sustainable agriculture (Pereira *et al.*, 2018; Naorem, 2022; Taguchi, 2023, 2023). This is particularly relevant to rewilding projects, which aim to restore ecosystem and soil health in degraded landscapes by means of trophic cascades. By aiming to enhance soil carbon levels, these projects hope to support not only biodiversity but also to provide a means to fund conservation initiatives through climate finance (Griscom *et al.*, 2017). Carbon credits, therefore, create a tangible financial value for efforts that promote carbon capture and sustainable ecosystem management, making them a key tool in global conservation strategies (Taguchi, 2023; Telo Da Gama, 2023).

However, carbon credits are not without limitations. Challenges in accurately measuring soil carbon levels can undermine the effectiveness of these programs and their subsequent impact. The lack of standardized methodologies for soil carbon assessment makes it difficult to compare results across different regions and projects (Paul *et al.*, 2021; Steinhoff-Knopp, Kuhn and Burkhard, 2021). Additionally, the reliability of issued credits is often questionable, as poorly verified credits may not represent genuine reductions in atmospheric carbon. Further, temporary storage, where sequestered carbon is later released, further undermine the credibility of carbon credits. Addressing these limitations through improved verification standards, consistent methodologies, and rigorous monitoring is crucial for ensuring the integrity and effectiveness of carbon credit markets now and into the future (Baveye, Baveye and Gowdy, 2016; Taguchi, 2023; Oberreich *et al.*, 2024).

1.7: Market and Economy

The green economy is a concept that focuses on sustainable and responsible economic growth at both global and local scales. It emphasizes development that is socially and environmentally sound, recognizing that longevity is key to long-term financial, environmental, and societal success (Anikwe and Ife, 2023). However, the concept is considered highly controversial, primarily because definitions of the green economy vary widely (Baveye, Baveye and Gowdy, 2016). Despite this, a green economy approach underscores the importance of environmental sustainability in future development and, by extension, highlights the need for biodiversity conservation as a cornerstone of economic progress (Keesstra *et al.*, 2018). Traditionally, the green economy concept focuses on large-scale policies and international frameworks (Keesstra *et al.*, 2018; Paul *et al.*, 2021). While such policies are essential, local solutions are equally critical to achieving these broader goals. This is where a nature-based economy, also known as nature-based solutions, comes into play. Unlike the high-level parts of the green economy, a nature-based approach emphasizes small-scale, practical implementation of sustainable practices (Keesstra *et al.*, 2018). However, it's worth noting that these concepts are supplementary to one another, rather than diametrically opposed.

Nature-based solutions encompass strategies like protected areas, ecotourism, rewilding, sustainable agriculture, and ecosystem restoration. These solutions prioritize ecosystem health and the sustainable utilization of natural resources, offering pathways for communities to prosper economically while preserving their environment. Biodiversity and carbon credits can provide financial incentives, promoting a shift in thinking toward more responsible resource management as a result of compensation for effective stewardship (Taguchi, 2023). Rewilding projects, for instance, can enhance carbon sequestration by restoring natural ecosystems, potentially generating carbon credits to fund further conservation efforts. This creates a positive feedback loop where restored ecosystems not only support biodiversity but also contribute to climate mitigation and empowering communities and land owners (Keesstra *et al.*, 2018).

The contrast between green economy policies and nature-based economy implementation is significant. While green economy policies set the vision, nature-based approaches provide the practical tools to achieve it. Together, there is the potential to foster a balanced system where large-scale policy frameworks are supported by localized actions, ultimately driving meaningful and lasting progress toward sustainability.

1.8: Aims, objectives, and hypotheses

Aims

This study aimed to evaluate the impact of Megafauna reintroduction on the ecosystem health of two semi-arid ecosystems (Klein Karoo and Renosterveld) by evaluating changes in physical and chemical soil characteristics, vegetation composition and dung beetle diversity in Sanbona Wildlife Reserve. One of the main driving forces behind the reserve's conception was to restore and then conserve the natural ecosystems of this semi-arid region after decades of agricultural use. I compared these ecosystem-health proxies across areas with different faunal communities (Megafauna, Mesoherbivores and Livestock) between two vegetation types (Renosterveld and Klein Karoo).

Objectives and hypotheses

Main Hypothesis

I hypothesize that the various ecosystem-health proxies will be similar between livestock and mesoherbivore areas due to the similar body sizes and feeding behaviours, but that megafauna areas will be significantly different due to larger body size and subsequent impact on vegetation structure by these animals through grazing habits and movement.

Supporting objectives and hypotheses

1) To investigate the impact of reintroduced megafauna on soil health by measuring key physical and chemical indicators such as pH, bulk density, organic matter, and several nutrient levels.

- I hypothesise that megafauna areas will exhibit enhanced nutrient cycling, higher levels of organic matter, and lower bulk densities compared to mesoherbivore and livestock areas, due to their distinctive feeding and trampling behaviours.

2) To assess the impact of megafauna on vegetation functional types.

- I hypothesise that megafauna areas will display greater heterogeneity in plant functional types, due to the creation of diverse niches through grazing, browsing, and trampling, which promote both herbaceous and woody growth.

- Conversely, I hypothesise that livestock areas will show the highest levels of vegetation homogeneity, as continuous grazing selects for a limited number of grazing-tolerant plant species.

3) To assess the impact of megafauna on vegetation production using Enhanced Vegetation Index (EVI).

- I hypothesise that the open vegetation structure created by megafauna will support productive grasses and stimulate new green growth in woody plants, resulting in higher EVI values.
- I further hypothesise that megafauna areas will show the greatest vegetation heterogeneity and therefore the highest EVI scores, while livestock areas will show the most homogeneous vegetation communities and the lowest EVI scores.

4) To determine the effects of treatment (Megafauna, Mesoherbivores, and Livestock) on dung beetle diversity and abundance.

- I hypothesise that dung beetle diversity and abundance will be highest in megafauna areas, owing to the greater availability and variety of dung compared to mesoherbivore and livestock areas.

5) To quantify and contrast the overall effect of rewilding on ecosystem health in different ecosystem types.

- I hypothesise that the impact of rewilding will be more pronounced in the Klein Karoo than in the Renosterveld, due to differences in rainfall, soil type (nutrient-poor in the Klein Karoo vs nutrient-rich in the Renosterveld), and the resulting differences in vegetation structure and composition.

6) To evaluate the viability of carbon credits as a conservation funding tool for rewilding projects in semi-arid areas.

- I hypothesise that soil carbon levels will be higher in megafauna areas across both vegetation types, indicating that rewilding may offer a credible pathway for generating carbon credits in degraded semi-arid landscapes.

7) To provide recommendations for conservation strategies which seek to address habitat degradation, through rewilding, in semi-arid areas.

METHODS AND MATERIALS

Study site

2.1: Sanbona Private Wildlife Reserve

At over 60 000 hectares, Sanbona Private Wildlife Reserve is a privately owned wildlife reserve found in South Africa’s Western Cape Province, roughly 64 km east of Montagu. The reserve lies at 33°43’24’’ S and 20°36’55’’ E, spanning approximately 25 km from north to south and 30 km from east to west at its widest and was established in 2002. The reserve is divided by the Warmwaterberg Mountain range, an east-to-west geological feature that separates the area into Sanbona North (24 600 hectares) and Sanbona South (23 500 hectares). This division has facilitated distinct management strategies for wildlife and tourism, owing, at least in part, to the very different edaphic, rainfall and resulting vegetation types found in each segment (Vorster, Hoffman and Todd, 2017; Swanepoel and Alison, 2019, Fig. 1).

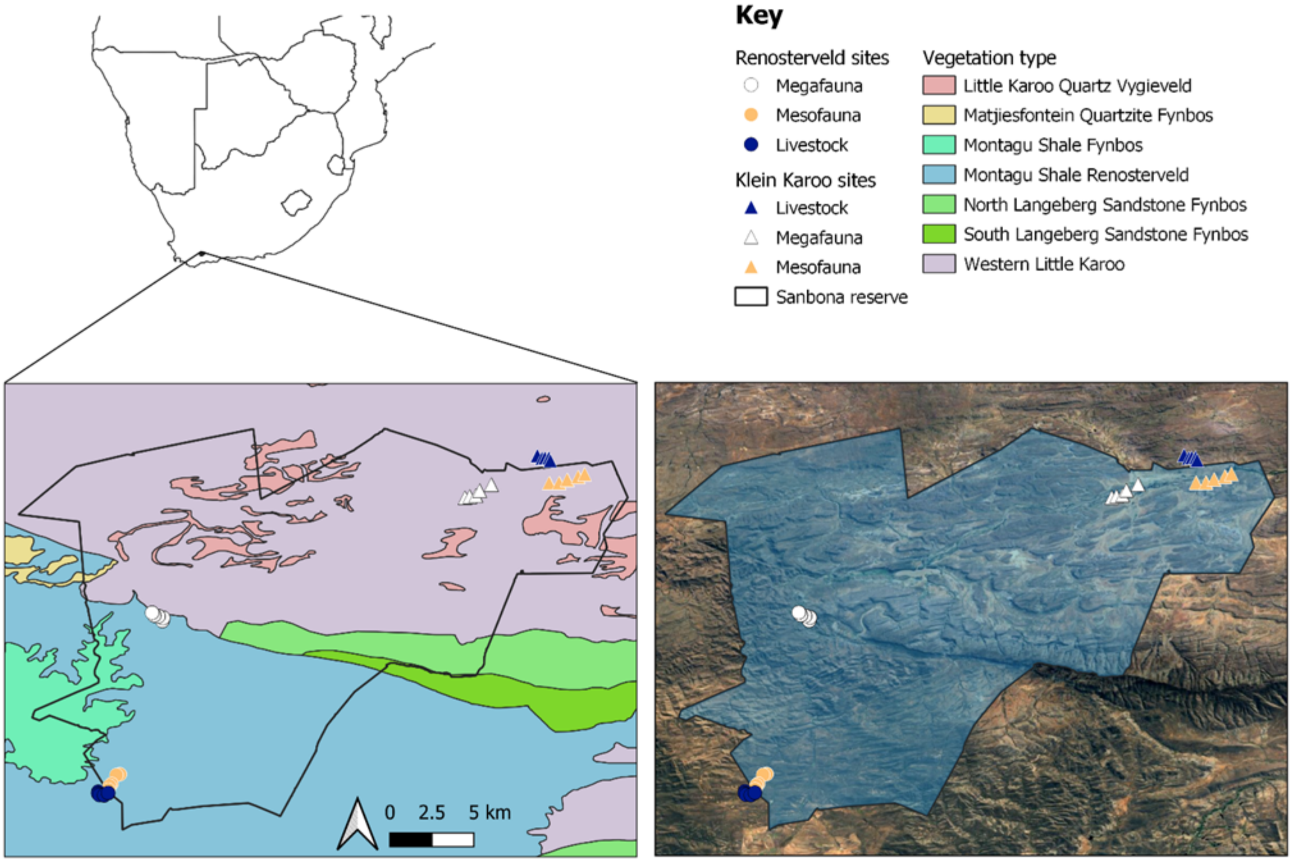

Figure 1. Map showing the location, sample sites and vegetation types of Sanbona Wildlife Reserve.

The Warmwaterberg range forms part of the Table Mountain Group, composed mainly of sandstone and quartzite, which results in predominantly acidic and nutrient-poor soils. The surrounding hills and valleys belong to the Bokkeveld Group and Witteberg Group, consisting of sandstones and mud-rock that produce nutrient-rich soils. The elevation on the reserve varies from 430 m above mean sea level (a.s.l.) in the Brak River valley to 1 344 m a.s.l. at the highest peaks of the Warmwaterberg (Vorster, Hoffman and Todd, 2017; Swanepoel and Alison, 2019). The reserve encompasses two main vegetation types: Montagu Shale Renosterveld on the nutrient richer soils in the southern section, and Western Klein Karoo on nutrient poorer soils in the northern section. These vegetation types contribute significantly to the 600 plant species found within Sanbona, distributed across 12 habitat types such as Apronveld, Quartz Vygieveld, Gannaveld, Central Mountain Fynbos, Thickets, and Succulent Karoo (Mucina and Rutherford, 2006). The unique combination of geology, rainfall variability, and elevation supports a high diversity of plant life, including species adapted to semi-arid conditions, such as *Dicerothamnus rhinocerotis* (renosterbos), various succulents, and grasses (Vorster, Hoffman and Todd, 2017; Swanepoel and Alison, 2019).

Sanbona’s climate is classified as semi-arid and lies within a transition zone between winter and summer rainfall regions. Winter rainfall, occurring from June to August, is primarily cyclonic (frontal), while summer rainfall, from November to March, results from thunderstorms (convectional). The northern section of the reserve experiences a rain shadow effect due to the Warmwaterberg mountains, receiving around of 195 mm of rainfall annually, compared to 315 mm in the southern section. Historical data shows variability in rainfall patterns, with drought cycles recorded between 2008 and 2010, followed by improved rainfall between 2011 and 2015. In 2016, rainfall fell to 109 mm in the north and 160.9 mm in the south. This trend continued in 2017, with only 98 mm recorded in the north and 177.2 mm in the south. Temperatures range from -2°C to 41.8°C, with mean maximums of 30.6°C in summer and mean minimums of 4.9°C in winter. Frost is common on winter mornings due to clear skies and low overnight temperatures (Vorster, Hoffman and Todd, 2017; Swanepoel and Alison, 2019). Water resources within the reserve are limited and depend heavily on rainfall. The primary sources of water include seasonal rivers such as the Brak River, Matjiesbos, Kalkoenshoek, and Gatskraal, as well as the Bellair Dam and several artificial water points (AWPs). Natural springs also provide water but are seasonal and influenced by annual rainfall patterns (Swanepoel and Alison, 2019).

History of management

Before its establishment as a conservation area in 2002, Sanbona was used extensively for wheat and livestock farming. These agricultural practices significantly impacted the landscape as well as the soil, particularly in the Montagu Shale Renosterveld, where approximately 2 000 hectares were cleared for cultivation. These previously farmed areas, now known as Old Lands, have lower plant diversity and are characterized by the presence of alien and invasive species

(Shiponeni and Milton, 2006; Vorster, Hoffman and Todd, 2017). In 2002, Sanbona was converted into a wildlife reserve with the goal of restoring the natural ecosystem through the process of rewilding. This involved the reintroduction of indigenous megafauna, including elephants (*Loxodonta africana*), white rhino (*Ceratotherium simum*), black rhino (*Diceros bicornis*), buffalo *(Syncerus caffra*), giraffes (*Giraffa camelopardalis*), and various mesoherbivore antelope species such as cape eland (*Tragelaphus oryx*) and greater kudu (*Tragelaphus strepsiceros*). The reserve was divided into Sanbona North and Sanbona South by internal fencing along the Warmwaterberg range. This separation facilitated specific management practices, with two independent herds of elephants and buffalo in the northern and southern sections. The reserve's water resources include seasonal rivers, artificial water points, and natural springs, which are essential for sustaining wildlife, especially during periods of drought (Vorster, Hoffman and Todd, 2017; Swanepoel and Alison, 2019).

In the Montagu Shale Renosterveld section (South) where the land has had a long history of agricultural use, including sheep and cattle farming, Nguni cattle were introduced, and regenerative livestock management practices were implemented since 2002. These practices involve high intensity grazing in temporary camps that are strategically moved to avoid overgrazing. The cattle graze the land intensively before being relocated, with the assumption that this would promote the return of native grass species and soil regeneration. Currently, these areas are dominated by shrub growth, and the management approach aims to restore the balance of grass and shrub cover (Liesl Vorster, 2024, pers. comm).

In the Western Klein Karoo section, former livestock areas previously grazed by Bonsmara cattle have been left to rest for the past six years to allow for natural recovery. Additionally, some regions within the Klein Karoo were historically used for lucerne cultivation, a nitrogen-fixing legume. While sampling was carefully conducted to avoid these areas, remnants of old man's saltbush (*Atriplex nummularia*), an Australian fodder crop, remain in some locations. These historical practices may have led to elevated nitrogen levels in the soil, particularly in areas where lucerne- a legume- was grown. Despite these potential nutrient imbalances, efforts were made to focus on areas minimally impacted by past agricultural activities (Liesl Vorster, 2024, pers. comm).

Site Selection

Generally, and as far as possible, efforts were made to focus on areas minimally impacted by past agricultural activities to avoid confounding factors that might affect our proxy measurements. Similarly, care was taken to avoid riverbeds and areas of obvious previous agricultural activity.

A total of 30 sites were selected across the study area, divided between two dominant vegetation types- Montagu Shale Renosterveld in the south and Western Klein Karoo in the north, thus a total of 15 sites in each vegetation type (Fig. 13). Within each vegetation type, the sites were further categorized into three distinct zones based on the presence and type of herbivores: 1) Megafauna areas, dominated by large herbivores such as elephant, buffalo and rhino. 2) Mesoherbivores areas, hosting ungulates up to and including giraffe and 3) Livestock areas, characterised by the presence of domestic livestock, in this case, cattle. This approach resulted in a total of 10 sites per category (five in Renosterveld, five in Klein Karoo), providing a variety of herbivore activity for comparison. These zones of herbivores were identified by a previous study (Swanepoel and Alison, 2019), which provided baseline data on herbivore distributions. The study had identified areas where each elephant herd (North and South Herd) had spent 95% of their time during a given period. Thus, I generated randomized points within this high-concentration zone in the respective megafauna areas using ArcGIS, to reduce biased sampling Megafauna areas. The same process was then followed for the Mesoherbivores and Livestock areas respectively. To ensure site comparability and livestock areas. A minimum distance of 800m was maintained between sites to reduce spatial autocorrelation. So that herbivore categories were comparable, sites were of similar elevation, soil, and vegetation type as far as possible. Further, care was taken to avoid riverbeds and areas of obvious previous agricultural activity, to avoid sample contamination and ensure comparability.

2.2: Soil Sampling and Analysis

A total of 120 soil samples were collected across 30 different sites (n = 4 per site) to analyse selected soil chemical and biological characteristics (Fig. 2). At each site, bulk soil was collected to 200 mm depth using an auger (∅ 100 mm). One bulk soil sample comprised 3 cores taken ca. 1-2 m apart that were homogenised and sub-sampled into labelled bags and subsequently air-dried. Soil chemical characteristics (ammonium (NH_4^+), nitrate (NO_3^-), organic carbon, active carbon, and organic matter) were determined on all 120 air-dried, bulk soil samples by a commercial laboratory (Sporatec, Stellenbosch University, South Africa). Briefly, nitrate and ammonium were measured on soil extracts (2 M KCL) via routine spectrophotometric methods based on the indophenol method (López et al. 2007; Griffin et al. 2011) and azo dye method (Bolleter et al. 1961; Zhou and Boyd, 2016) respectively. Organic matter was measured using the loss on ignition method (USDA NRCS 2014), soil organic carbon was measured using the

Walkley Black method (Anderson and Ingram 1994) and active carbon was measured using the permanganate oxidizable carbon method (Weil et al. 2003). Active carbon is an indicator of the fraction of soil organic carbon that is readily available as an energy source for soil microbes during decomposition. It is thought to respond more rapidly that other soil organic carbon fractions to changes in management. Soils did not contain carbonates and thus did not require acid fumigation prior to soil organic carbon analysis.

A total of 30 soil sample were collected across 30 sites (n = 1 per site) for in-house analysis of selected soil physical characteristics. Bulk density was measured by collecting intact soil into 103-cm^3 metal rings (Eijelkamp bulk density kit). Fine earth bulk density of soil was expressed in g cm^{-3} by measuring the dry soil mass (60°C) and dividing this by the known volume (103-cm^3) of the soil ring, after accounting for any stones or root biomass. Soil pH was measured by mixing 20 g air-dried soil in 50 mL 1-M KCL on a reciprocal shaker (100 rpm) for 1 h before measuring pH in the clear supernatant. Soil particle size distribution was measured by laser diffraction using a Malvern Mastersizer and Hydro 2000G (Malvern Panalytical, Almelo, Netherlands). Multiple particle sizes were binned into categories of sand, silt and clay based on the standard US Department of Agriculture (USDA NRCS 2014) classification system.

Analysis was focused on key nutrient indicators (pH, Ammonium, Nitrate, Active Carbon, Organic Carbon, and Organic Matter) as well as the main physical characteristics (Bulk Density and Bareground percentage). Soil health is a vital part of overall ecosystem health. By quantifying the differences in the important characteristics listed above, between treatment types, it’s possible to illustrate the potential impact of rewilding on soil health and by extension, ecosystem health. Further, these analyses were done across vegetation types, allowing for the comparison of how rewilding impacts ecosystem health differently across different ecosystems.

To test the stated hypotheses, I generated Generalised Linear Models, an approach robust to non-normally distributed data, to investigate the changes in variables, between treatments, for both vegetation types. Elevation was used as a covariate in each case. When significant differences were observed, pairwise analysis was performed to identify where significant differences occurred and to what degree.

2.3: Pitfall Traps and Analysis

Dung beetles were sampled using pitfall traps across 30 different sites, with a total of 120 traps deployed (four traps per site). At each site, four 2L buckets were buried in the ground to the brim to serve as the trap (North, South, East and West). A piece of elephant dung, collected the night before, was suspended over each trap using sticks. Fresh elephant dung had been bagged and frozen to ensure consistency and reduce degradation. Each trap contained a mixture of propylene glycol and water at the bottom to prevent beetles from escaping once they fell in. The traps were left in place for a 24-hour period, after which the buckets were sealed and collected. One replicate (1N) was accidentally left out for a period of 48 hours and was thus removed from the analysis.

The traps were processed in the laboratory. The samples were poured onto a wire mesh to separate the beetles from other debris. Dung beetles were sorted to morphospecies and pinned for identification by a dung beetle specialist (A. Davis).

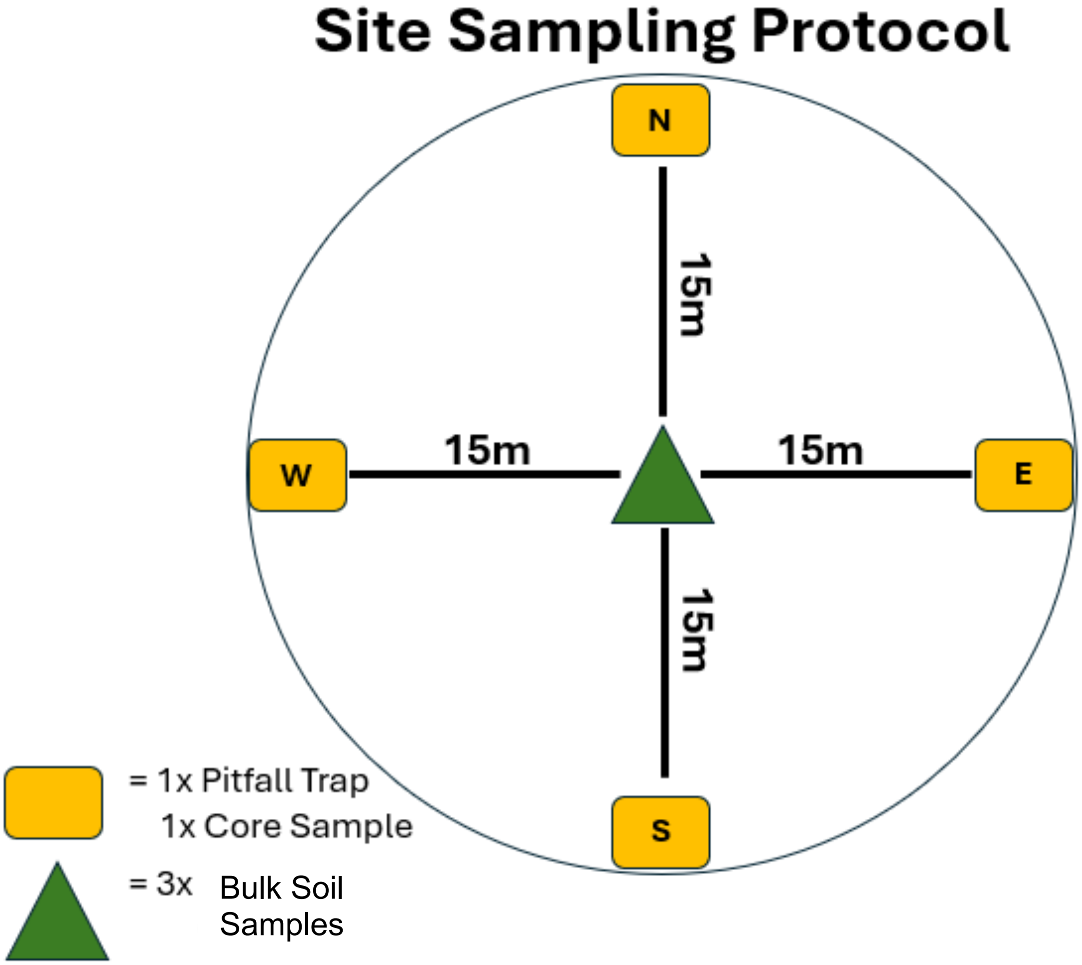

Figure 2. Site sampling protocol.

2.4: Vegetation cover and EVI

At each of the 120 replicates across the 30 study sites, a 1m x 1m grid was placed on the ground to assess vegetation species composition and surface composition (litter, bare ground, vegetation cover). A photograph was taken of each grid, which was later analysed visually to identify and quantify the proportions of bare ground, rock, litter, grass, shrubs, and succulents per replicate. Each photograph was independently evaluated by three researchers, and any discrepancies in the estimated proportions were resolved through discussion until a consensus was reached, ensuring consistent and reliable data collection. This method provided a rapid and reasonably accurate assessment of the mix and coverage of vegetation and non-vegetation components in the study areas (Parr *et al.*, 2004).

Additionally, an Enhanced Vegetation Index (EVI) analysis was performed to compare current vegetation conditions to those from 20 years ago. This historical comparison helped to quantify changes in vegetation cover and identify trends related to rewilding efforts, grazing management, and ecological recovery within the reserve. Twenty-four years (2001-2024) of monthly EVI data were extracted for all 120 sample sites using the MODIS Terra Daily product (MODIS_MOD09GA_006_EVI) available via the Google Earth Engine Platform (Gorelick et al 2017). Data processing of EVI is described under Statistical Analyses.

2.5: Statistical Analyses

I explored the relationships among environmental and soil variables in order to better understand underlying patterns and relationships present in the system. Principal Component Analysis (PCA) was used to understand how the data grouped and which variables were most influential across treatment and vegetation types. Non-metric Multidimensional Scaling (NMDS),on the other hand, was used to visualize dissimilarities. These methods help reveal broad trends in how the numerous variables and their impacts vary across different treatments and vegetation types.

The Scree plot is included and was used to understand how much variance is explained by each dimension, with the bulk of the variance being explained by Dimensions 1-3 (Fig. 11). Contribution graphs were then used to evaluate the top contributors to each dimension. For each PCA generated, the top 5 contributors to each are provided, along with directionality arrows.

PCAs and NMDSs

All analyses were conducted in R V4.4.1 (R Core Team, 2024) The main packages used for this analysis were tidyverse (Wickham et al., 2019), FactoMineR (Le et al., 2008) and knitr (REFS). Besides all Xie, 2015). Data on soil and vegetation variables were compiled from an Excel spreadsheet using the measured variablesreadxl (Wikcham & Bryan, 2023) package. After removing unnecessary columns, a composite variable “SoilTexture” was generated using Sand, Silt, and Clay measurements and used for further analysis. For the overall dataset, numeric variables were extracted and subjected to PCA using the FactoMineR (Le et al., 2008) package. The PCA results were visualized through biplots, scree plots, and variable contribution plots, with additional customized biplots created to display groupings by Treatment, Vegetation Type, and their combination. Separate PCA analyses were also conducted on the Klein Karoo and Renosterveld subsets to further examine treatment effects within each vegetation type. For each PCA, the contributions of variables to the first few dimensions were tabulated and visualized.

Non-metric multidimensional scaling (NMDS) was performed using the vegan package (Oksanen et al., 2022) on the same set of numeric variables to explore multivariate patterns. NMDS analyses were conducted using Euclidean distances, with the number of dimensions set to two and three in different iterations. A seed was set to ensure reproducibility. NMDS site scores were extracted and plotted using ggplot2 (Wickham, 2016) for Treatment, Vegetation Type, and their combination. Additionally, environmental vectors were fitted to the NMDS using the envfit function, and only those variables with significant correlations ($p < 0.05$) were displayed.

Box and whisker plots

Elevation was scaled so as not to over-estimate its impact. The dataset was then split by vegetation type into two groups: "Klein Karoo" and "Renosterveld." For each subset, percentage values for variables such as Bare ground, Grass, Succulents, Shrubs, and Litter were converted to proportions (to give a value between 0 and 1). Generalized Additive Models (GAMs) were fitted with the mgcv package (Wood, 2017) to investigate the effects of *Treatment* and an environmental covariate (Elevation) on several soil and vegetation response variables, as well as dung beetle abundance.

For the "Klein Karoo" subset, models generally followed the form “Response~Treatment + s(Elevation,bs="ts") + s(Site,bs="re")”, where Treatment is treated as a fixed effect, while smooth terms were used for Elevation and *Site* (set as a random effect) in order to control for spatial variability. For the "Renosterveld" subset, the same model outline was generally used, except where Elevation was excluded for purposes of model fit and accuracy. For each model, summary statistics were examined, and the estimated marginal means were computed using the *emmeans* package (Lenth, 2024). Pairwise comparisons were then done between treatments in order to assess differences and the significance of those differences. In addition, quantiles (25th, 50th, and 75th percentiles) of the response variables were calculated for evaluation purposes. Unless stated otherwise, Gaussian GAMs were used. Exceptions to this are dung beetle diversity, where negative binomial was used, and vegetation variables (Bare ground, Litter, Grass, Shrubs, Succulents) where beta regression (betar family) was used. In order to visualise the above models, box and whisker plots were created using ggplot2 (Wickham, 2016). Compact letter displays (CLDs) were extracted from the pairwise comparisons done previously using the *multcompView* package. These letters were applied to the plots and used to summarize statistically significant differences between treatments. To generate a contrast table, all treatment comparison outputs were stored in a named list. Then, using the purrr package (Henry & Wickham, 2023), the pairwise contrasts were extracted using the pairs() function.

EVI Calculations

The main packages used for this analysis were pacman (Rinker, 2023), raster (Hijmans, 2024), terra (Hijmans, 2024), dplyr (Wickham et al., 2023), tidyvers (Wickham et al., 2019), strigr (Wickham, 2023), ggplot2 (Wickham, 2016), sf (Pebesma, 2018), ggpubr (Kassambara, 2023) and lubricate Grolemund & Wickham, 2011).

Enhanced Vegetation Index (EVI)

The MODIS-derived raster files were read and processed using the *raster* (Hijmans, 2024), *terra* (Hijmans, 2024), and *tidyverse* (Wickham et al., 2019) packages. A custom ggplot2 (Wickham, 2016) theme was outlined and used to standardize plot aesthetics throughout the analysis. The EVI data for each year were extracted by stacking the respective yearly rasters and back-transforming by a factor of 0.0001 to obtain the correct scale. Mean annual EVI values were extracted for each site using the raster stack previously created. Mean annual EVI values were then associated with the respective vegetation types and treatments per site. A plot was generated to illustrate the change in EVI over time for each treatment. Annotations in red text indicate drought periods (2008–2010 and 2015–2016). Only annual and not monthly EVI is presented for ease of visualisation.

Carbon calculations

To determine soil organic carbon levels to investigate the potential viability of carbon credits as a conservation funding tool, I hypothesised that areas with reintroduced Megafauna would exhibit higher carbon levels compared to Mesoherbivores and Livestock areas across both vegetation types. This expectation is based on the premise that Megafauna enhance nutrient cycling and promote greater accumulation of organic matter, thereby increasing carbon sequestration.

By quantifying and illustrating differences in soil organic carbon between treatment types, this analysis seeks to investigate the ecological benefits of rewilding while also evaluating the economic potential of utilizing carbon credits for rewilding projects in semi-arid areas.

The soil organic carbon (SOC) content, expressed in tons per hectare (t ha^{-1}), was calculated for each treatment within the Klein Karoo and Renosterveld vegetation types (Table S2). SOC values were derived using the formula:

$$SOC\ (t\ ha^{-1}) = Organic\ Carbon\ (\%) \times 10 \times Bulk\ Density\ (g\ cm^{-3}) \times Soil\ Depth\ (m) \times 10$$

Where SOC (%) was converted to g kg^{-1} by multiplying ×10, bulk density was derived from the dataset, soil depth was 0.2 m, and a multiplier of 10 was applied to convert values from kg m^{-2} to t ha^{-1}. The main package used in this analysis was *dplyr and emmeans* along with appropriate scaling factors (scale) to ensure unit consistency. SOC values were compared per vegetation type and treatment.

RESULTS

3.1: Exploratory Statistics

For both PCAs, Klein Karoo and Renosterveld treatments clustered separately (Fig. 3 and Fig. 10). For the first PCA (Fig. 3) the five most influential variables were active carbon, pH and bare ground, organic matter and elevation. This suggests that Klein Karoo (particularly Mesoherbivores and Livestock treatments) have higher pH and active carbon, while Megafauna shows the highest levels of organic matter. In contrast, Renosterveld treatments clustered closely and were separated from the Klein Karoo mainly due to the influence of elevation. The second PCA (Dim1 vs Dim3 Fig. 12) shows similar results, however, shrubs and bulk density replace pH and bare ground. Both Megafauna treatments show low bulk density trends, Renosterveld also shows higher shrubs occurrence when compared to Klein Karoo.

NMDS was used to visualize the similarities and differences between sites with the arrows illustrating the most important variables, their direction of influence and magnitude. The NMDS largely supported the trends seen in the PCAs. Klein Karoo clusters were characterized by higher pH, greater dung beetle diversity (a new finding) and higher bare ground levels. In contrast, Renosterveld is characterized by higher elevation and greater shrub cover.

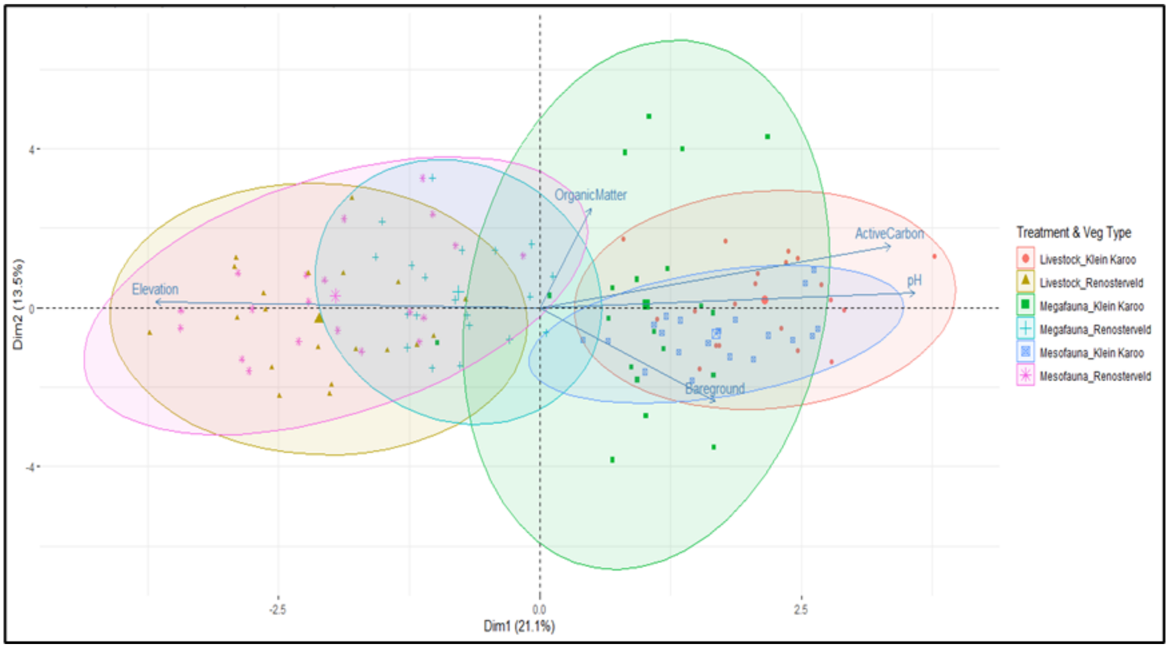

Figure 3. PCA of all factors per treatment and vegetation types (Dim 1(13.5%) vs Dim 2 (21.1%)).

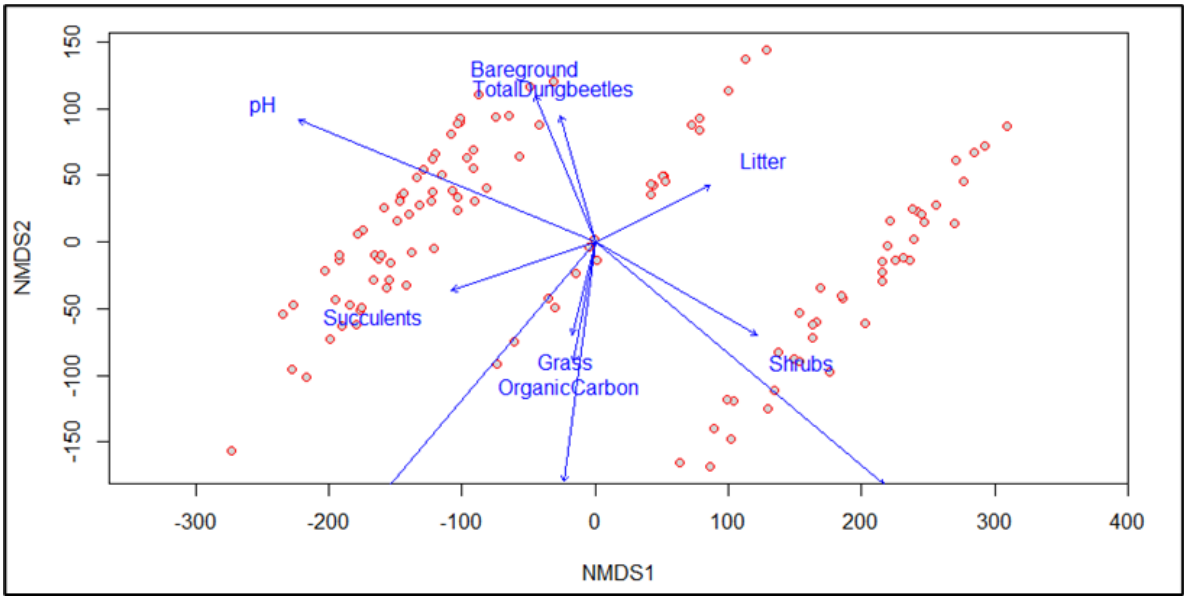

Figure 4. NMDS showing the eight key variables.

3.2: Soil

Renosterveld

Bulk Density

The highest mean bulk density in the Renosterveld is found in the livestock treatment (1.56 ± 0.07), followed by Megafauna (1.38 ± 0.12) and Mesoherbivores (1.33 ± 0.14), with the latter two showing more variability (Fig. 5, Table S2). Pairwise comparisons (Table S1) revealed significant differences in bulk density between Livestock and Megafauna (estimate = 0.18414, SE = 0.0366, $p < 0.0001$) and between Livestock and Mesoherbivores (estimate = 0.23394, SE = 0.0366, $p < 0.0001$). There appears to be no significant difference between Megafauna and Mesoherbivores (estimate = 0.04980, SE = 0.0366, p = 0.368).

pH

As shown in Table S2, the highest mean pH in the Renosterveld is found in the Megafauna treatment (6.48 ± 0.20). This is followed by Mesoherbivores (6.22 ± 0.31) and Livestock(5.93 ± 0.16), with Mesoherbivores showing more variability. Pairwise comparisons (Table S1) revealed significant differences in pH between Livestock and Megafauna (estimate = -0.5545, SE = 0.0742, $p < 0.0001$) and between Livestock and Mesoherbivores (estimate = -0.2945, SE = 0.0742, p = 0.00059). There were also significant differences between Megafauna and Mesoherbivores (estimate = 0.2600, SE = 0.0742, p = 0.0025).

These results show that the pH was significantly higher under the Megafauna treatment compared to both Livestock and Mesoherbivores. Further, the pH for Mesoherbivores is significantly higher than that of the Livestock control.

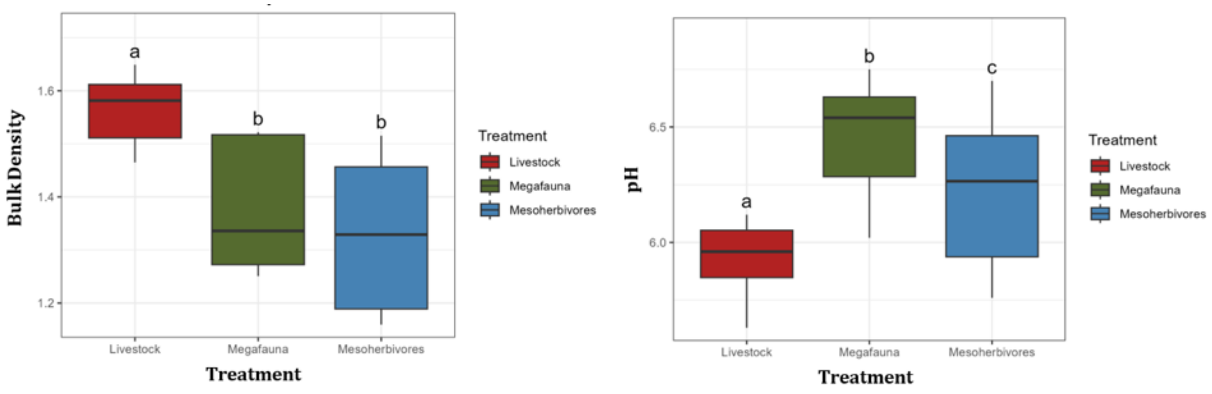

Figure 5. Box and Whisker plots with significance letters showing Bulk Density and pH for the Renosterveld vegetation type

Klein Karoo

Ammonium

As shown in Table S2, the highest mean ammonium levels in the Klein Karoo are found in the Megafauna treatment (0.71 ± 0.41, Fig. 6). This is followed by Mesoherbivores (0.58 ± 0.37) and Livestock (0.41 ± 0.27). Pairwise comparisons (Table S1) revealed a significant difference in ammonium levels between Livestock and Megafauna (estimate = -0.3035, SE = 0.1118, p = 0.0235). There were no significant differences between Livestock and Mesoherbivores (estimate = -0.1730, SE = 0.1118, p = 0.2770) or between Megafauna and Mesoherbivores (estimate = 0.1305, SE = 0.1118, p = 0.4776). These results indicate that ammonium levels are significantly elevated under the Megafauna treatment when compared to the Livestock.

Bare Ground

The highest mean bare ground cover in the Klein Karoo was observed under the Mesoherbivores treatment (66.10 ± 18.99), followed by Megafauna (57.90 ± 31.78) and Livestock (39.15 ± 22.15) (Table S2). Pairwise comparisons (Table S1) revealed no significant difference in bare ground cover between Livestock and Megafauna (estimate = -0.6636, SE = 0.3459, p = 0.1440). However, there was a significant difference between Livestock and Mesoherbivores (estimate = -0.9938, SE = 0.3472, p = 0.0162). No significant difference was observed between Megafauna and Mesoherbivores (estimate = -0.3302, SE = 0.3467, p = 0.6100). In this instance, estimates and standard errors are presented on the log odds ratio scale, not on the response scale. The results suggest that bare ground cover increases progressively from Livestock to Mesoherbivores and finally on to Megafauna, with a significant difference present Livestock and Mesoherbivores treatments (Fig. 4).

Bulk density

As shown in Table S2, the highest mean bulk density in the Klein Karoo is found in the Livestock treatment (1.52 ± 0.09), followed by Mesoherbivores (1.42 ± 0.07) and Megafauna (1.36 ± 0.07). Pairwise comparisons (Table S1) revealed significant differences in bulk density between Livestock and Megafauna (estimate = 0.1699, SE = 0.0006, p < 0.0001) and between Livestock and Mesoherbivores (estimate = 0.1293, SE = 0.0001, p < 0.0001). A significant difference was also observed between Megafauna and Mesoherbivores (estimate = -0.0407, SE = 0.0009, p < 0.0001). These results indicate that bulk density was significantly lower in the Megafauna and Mesoherbivores treatments compared to the Livestock control.

pH

As shown in Table S2, the highest mean pH in the Klein Karoo is found in the Livestock treatment (7.52 ± 0.16), followed by Megafauna (7.14 ± 0.20) and Mesoherbivores (6.76 ± 0.07), which also exhibits the least variability. Pairwise comparisons (Table S1) revealed significant differences in pH between Livestock and Megafauna (estimate = 0.8519, SE = 0.0811, $p < 0.0001$). There was no significant differences between Livestock and Mesoherbivores, although the p value is close to being significant (estimate = 1.1308, SE = 0.5170, $p = 0.0837$). There is no significant difference between Megafauna and Mesoherbivores (estimate = 0.2789, SE = 0.5028, $p = 0.8446$). These results indicate that pH was significantly lower under the Megafauna treatment, but not Mesoherbivores, when compared to the Livestock control.

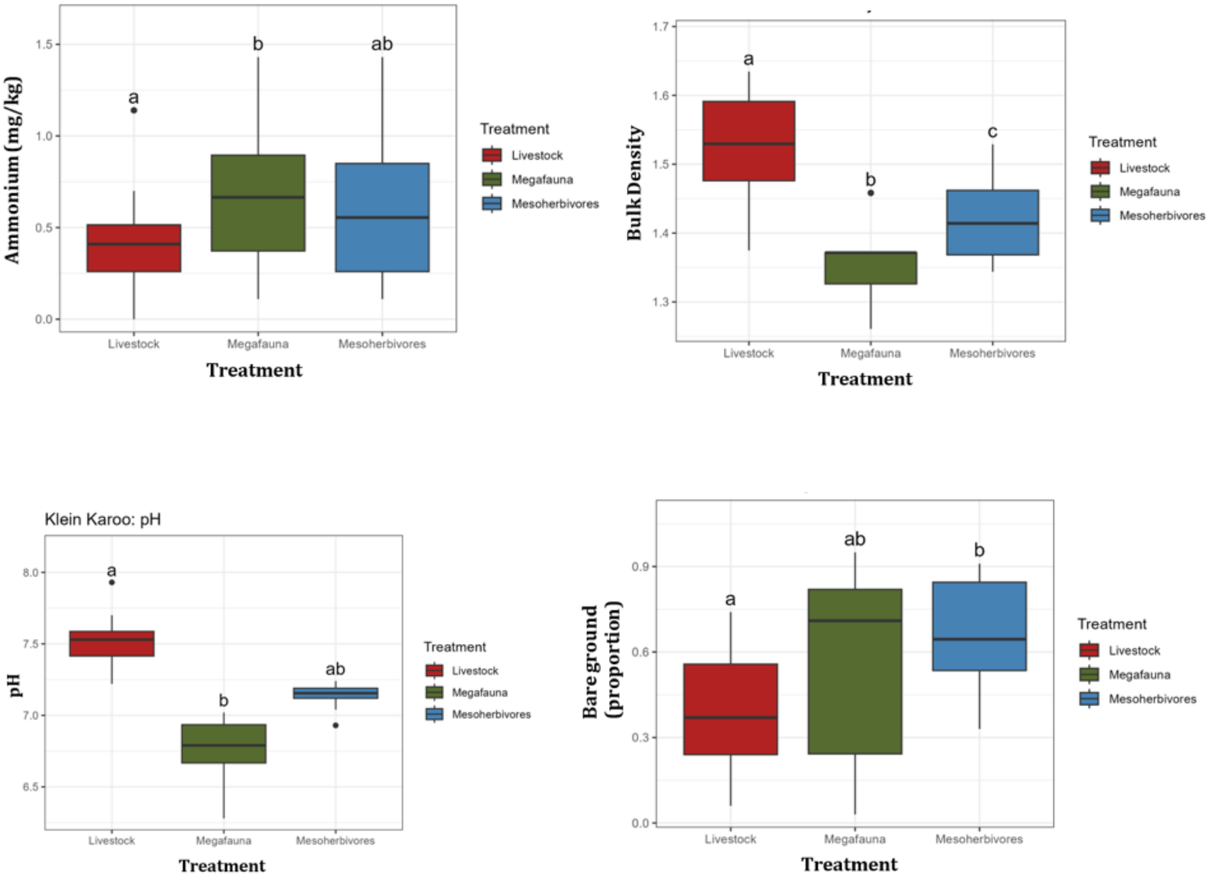

Figure 6. Box and Whisker plots with significance letters showing Ammonium, Bulk Density, pH and Bare ground for Klein Karoo vegetation type.

3.2: Biological Indicators (Dung Beetles)

Abundance

Klein Karoo

A total of 119 dung beetles and nine species were collected (Table S3), of which *Scarabeus viator* was the most abundant (Fig. 14). The highest mean dung beetle abundance in the Klein Karoo was observed in the Megafauna treatment (2.40 ± 3.89) (Fig. 7, Table S2). This was followed by Mesoherbivores (0.90 ± 1.89) and Livestock (0.65 ± 0.99). Pairwise comparisons (Table S1) revealed significant differences in total dung beetle abundance between Livestock and Megafauna (estimate = -3.6192, SE = 1.1455, p = 0.0074) and between Livestock and Mesoherbivores (estimate = -10.9086, SE = 3.5023, p = 0.0083). There were no significant differences between Megafauna and Mesoherbivores (estimate = -7.2894, SE = 3.1033, p = 0.0580), however, such a low p value suggests that these differences require further investigation. In this instance, estimates and standard errors are presented on the log odds ratio scale for ease of analysis, not on the response scale. Variability is particularly large in the Megafauna treatment. These results suggest that both the Megafauna and Mesoherbivores treatments have significantly greaterdung beetle abundance compared to the Livestock control.

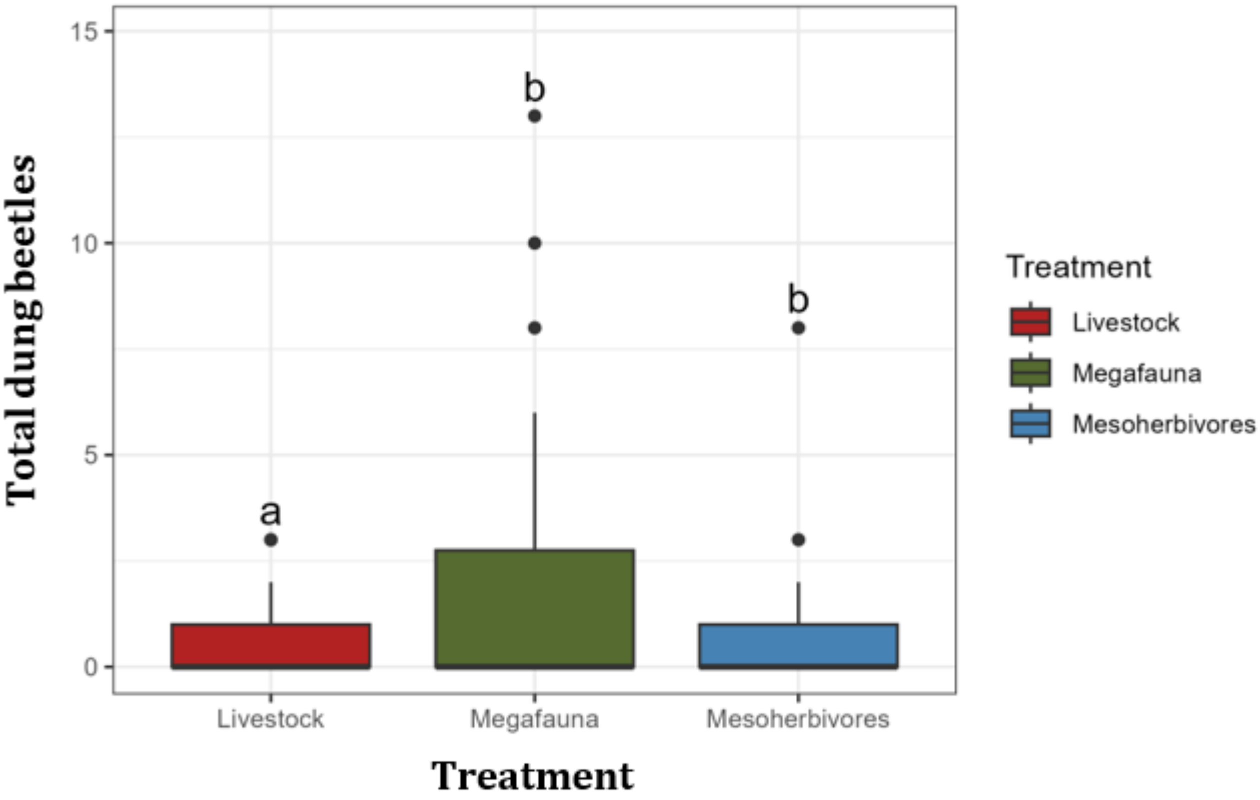

Figure 7. Box and Whisker plot with significance letters showing dung beetle abundance in the Klein Karoo vegetation type.

3.3: Vegetation

Klein Karoo

Shrubs

As shown in Table S2, the highest mean shrub percentage in the Klein Karoo was found in the Megafauna treatment (14.30 ± 19.18), which also displays the greatest amount of variation. This was followed by the Mesoherbivores treatment (8.60 ± 12.77) and Livestock (1.45 ± 2.60), which displayed the lowest shrub density, as well as variability (Fig. 8). Pairwise comparisons (Table S1) revealed significant differences in shrub cover between Livestock and Megafauna (estimate = -2.3039, SE = 0.5181, $p < 0.0001$). There was no significant difference between Livestock and Mesoherbivores, though the low p value does suggest that there may be a notable difference (estimate = -1.9494, SE = 0.8388, p = 0.0617). There is no significant difference between Megafauna and Mesoherbivores (estimate = 0.3545, SE = 0.7406, p = 0.8817). In this instance, estimates and standard errors are presented on the log odds ratio scale, not on the response scale. These results indicate that shrub density percentage was significantly higher in Megafauna, but not and Mesoherbivores when compared to the Livestock control.

Succulents

As shown in Table S2, the highest mean percentage of succulents in the Klein Karoo was observed in the Livestock treatment (23.40 ± 25.36), which also shows the highest amount of variability. This was followed by the Mesoherbivores treatment (9.35 ± 17.46) and the Megafauna treatment (3.55 ± 5.42), both of which exhibited substantially lower means with less variability. Pairwise comparisons (Table S1) revealed no significant differences in succulent cover between Livestock and Megafauna (estimate = 0.8359, SE = 0.4546, p = 0.1672). However, there was a significant difference between Livestock and Mesoherbivores (estimate = 1.1529, SE = 0.4530, p = 0.0364). No significant differences were observed between Megafauna and Mesoherbivores (estimate = 0.3170, SE = 0.4453, p = 0.7576). Estimates and standard errors are presented on the log odds ratio scale, not on the response scale. These results indicate that succulent abundance percentage was significantly higher under the Livestock treatment compared to the Mesoherbivores treatment, and that neither differed from Megafauna significantly.

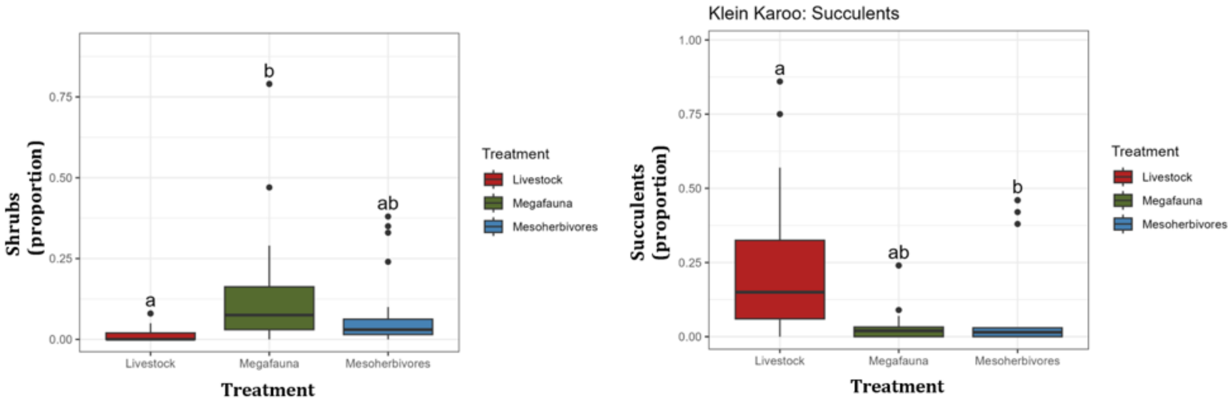

Figure 8. Box and Whisker plot with significance letters show shrub and succulent percentages in Klein Karoo vegetation type.

Renosterveld

Shrubs

As shown in Table S2, the highest mean percentage of shrubs in the Renosterveld was observed in the Livestock treatment (30.55 ± 30.53) which also showed the highest variability

(Fig. 9). This was followed by the Mesoherbivores treatment (28.65 ± 17.01) and the Megafauna treatment (11.55 ± 10.64), which exhibited the lowest mean with less variability. Pairwise comparisons (Table S1) revealed no significant differences in shrub cover between Livestock and Mesoherbivores (estimate = -0.4283, SE = 0.5764, p = 0.7392). However, there was a significant difference between Livestock and Megafauna (estimate = 1.3385, SE = 0.5799, p = 0.0640). Similarly, a significant difference was observed between Megafauna and Mesoherbivores (estimate = -1.7668, SE = 0.5790, p = 0.0101). Estimates and standard errors are presented on the log odds ratio scale, not on the response scale. These results suggest that the Mesoherbivores treatment maintains highest shrub coverage, while Megafauna has the lowest. The difference for shrub coverage for Livestock, when compared to either, is not significant.

Litter

As shown in Table S2, the highest mean percentage of litter in the Renosterveld was observed in the Megafauna treatment (40.70 ± 21.55), followed by the Mesoherbivores treatment (23.55 ± 20.47) and the Livestock treatment (21.15 ± 19.36), all of which display substantial variability. Pairwise comparisons (Table S1) revealed significant differences between the Livestock and Megafauna treatments (estimate = -0.9270, SE = 0.3210, p = 0.0152). However, no significant differences were observed between Livestock and Mesoherbivores (estimate = -0.1861, SE = 0.3275, p = 0.8376) or between Megafauna and Mesoherbivores (estimate = 0.7409, SE = 0.3183, p = 0.0605). However, the difference between Megafauna and Mesoherbivores is almost significant, suggesting that further investigation is needed. These results suggest that litter cover is significantly higher in the Megafauna treatment compared to the Livestock, while the Mesoherbivores treatment shows an intermediate response.

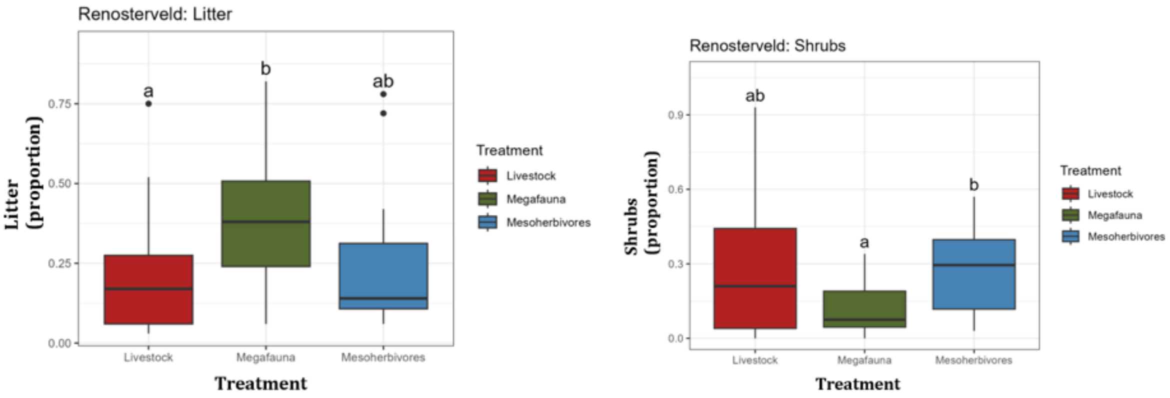

Figure 9. Box and Whisker plot with significance letter showing litter and shrub percentages for Renosterveld vegetation type.

The mean annual EVI varied across treatments and vegetation types over time, as illustrated in Figure 10. In the Klein Karoo, the Megafauna treatment consistently exhibited the highest EVI values across the time series, with notable peaks during wetter periods. These EVI values are substantially higher than those seen in the Mesoherbivores and Livestock treatment areas. In contrast, declines in the Megafauna EVI values during the drought periods of 2008–2010 and 2015–2016 are substantially greater in magnitude than those observed in the other treatments, with the Livestock areas showing the least amount of variability. The Mesoherbivores and Livestock treatments had showed lower EVI values, with the Livestock treatment generally exhibiting the lowest mean EVI across most years.

In Renosterveld, EVI values were relatively less variable across all treatments, with less pronounced differences between treatments compared to the Klein Karoo. However, the Megafauna treatment still tended to have slightly higher EVI values than Mesoherbivores and Livestock treatments. The 2008–2010 and 2015–2016 droughts corresponded to declines in EVI across all treatments, but the Renosterveld treatments showed a faster recovery compared to the Klein Karoo. However, the 2015-2016 drought shows a drastic lowering of EVI in the Megafauna area and a substantial lag period before returning to previous values.

Generally, changes in EVI appear to be more extreme in the Klein Karoo than in Renosterveld. Further, the impact of Klein Karoo Megafauna, in comparison to other treatments within the same vegetation type, appears to be greater than that seen in the Renosterveld. These patterns highlight how herbivore presence impacted vegetation differentially between vegetation types, over an extended period.

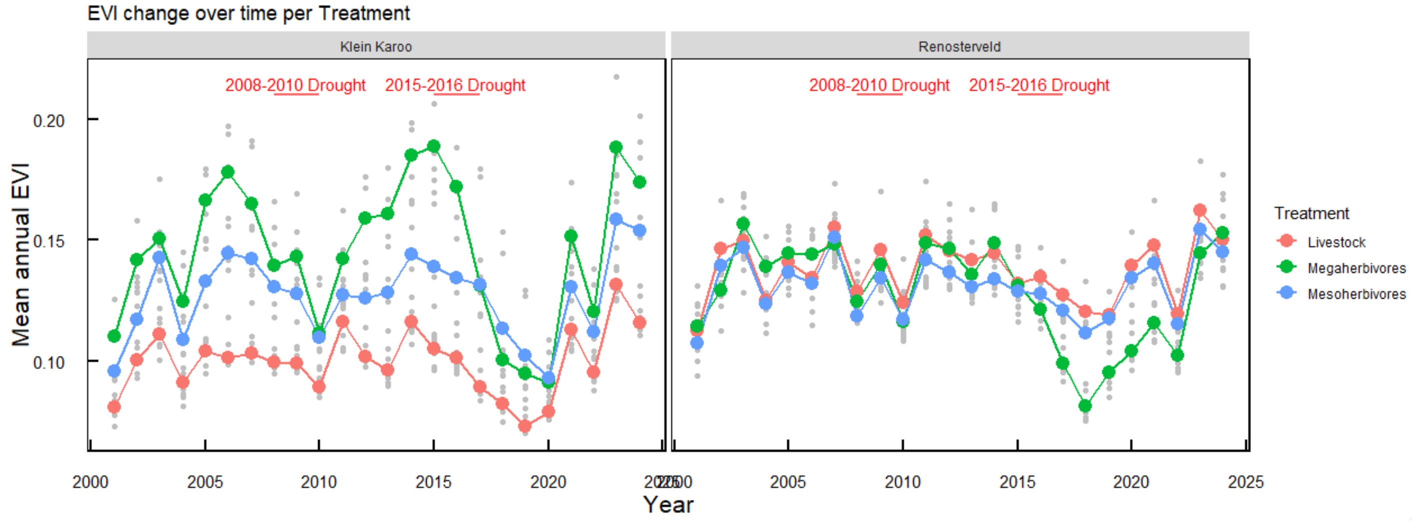

Figure 10. Enhanced Vegetation Index graph showing change in EVI over time per treatment.

3.5 Carbon stocks

In the Klein Karoo, the Livestock treatment yielded the highest SOC at 17.4 t/ha, followed by Mesoherbivores (13.6 t/ha) and Megafauna (13.3 t/ha). In contrast, Renosterveld shows that the Megafauna (15.9 t/ha) has the highest SOC, followed by Livestock (14.6 t/ha) and Mesoherbivores (14.0 t/ha) is lowest.

SOC dynamics differed across vegetation types. In the Klein Karoo, Livestock exhibits the highest SOC readings, while Megafauna shows the lowest. For the Renosterveld, Megafauna has the highest SOC readings, followed by Livestock and finally, Mesoherbivores. Livestock in the Klein Karoo has the highest SOC value among all treatments at 17.4 t/ha, which is roughly 2.8 t/ha (19.2%) higher than the equivalent in the Renosterveld and 1.5 t/ha (9.4%) greater than the Megaherbivore treatment in the Renosterveld.

Table 3: Summary of soil organic carbon per treatment.

Vegetation Type	Treatment	Soil Organic Carbon (t/ha)	Standard Deviation
Klein Karoo	Livestock	17.4	9.7
Klein Karoo	Mesoherbivores	13.6	6.8
Klein Karoo	Megaherbivores	13.3	7.6
Renosterveld	Livestock	14.6	8.2
Renosterveld	Mesoherbivores	14.0	11.0
Renosterveld	Megaherbivores	15.9	9.8

DISCUSSION

4.1: Overview

The impacts of rewilding are layered and complex. While intact ecosystems have generally been shown to be the most stable and resilient to adverse change, the influence and relative impact of important component ecosystem engineers (such as megafauna) is highly dependent on the abiotic ecological context. The composition of ecological communities and the interactions between these and their environment play a crucial role in determining how and how much reintroduced ecosystem engineers influence the system (Hobbs *et al.*, 2024). For this reason, it is critical for the management of rewilding that the complexity of these relationships is considered to improve understanding of the influence of rewilding on ecosystem functioning and health. This study has attempted to employ a holistic approach in building an understanding the impact of Megafauna reintroduction in the Sanbona area, by considering soil characteristics (physical and chemical), vegetation community composition, and invertebrate (dung beetle) abundance.

The approach uses two alternative ecosystem states, that of historical livestock management and mesoherbivore rewilding to assess the influences of megaherbivore reintroduction in the Sanbona, with the experimental landscape partitioned based on vegetation type, and accounting for key co-varying factors, namely elevation and - where possible - soil texture. Current vegetation cover for the various areas (Megafauna, Mesoherbivores, Livestock) was furthermore compared with that of two decades previously.

4.2: Soil Health

The impacts of rewilding on soil parameters differed to some extent between vegetation types, but certain overall consistencies in impacts were discernible. Bulk density, for example, is far higher in the livestock treatment areas for both vegetation types. This is likely due to an extended historical period of high stocking rates of cloved-footed ungulates with associated trampling effects (Lai and Kumar, 2020; Zhang *et al.*, 2024). Furthermore, while precise historical stocking rates for Sanbona were not available, it appears likely that these rates match relatively high stocking rates commonly used for high-intensity grazing with a single livestock type (of homogenous Livestock– solely cattle, *Bos taurus*), and would increase pressure on vegetation due to consistent grazing and vegetation selection, and subsequent compaction of soil. Most cattle breeds are obligate grazers, resulting in the high levels of grass biomass offtake, which I observed in these areas (Table S2) (Rahmanian *et al.*, 2019; Gebremedhn *et al.*, 2023). The combination of a lack of grass cover and increased trampling leads to high levels of compaction and therefore, comparatively higher bulk density readings in both Livestock areas (Lai and Kumar, 2020).

In contrast, lower bulk densities are seen in both Mesoherbivores and Megafauna areas. This is likely due to herbivore diversity, which not only leads to different and more evenly spread pressures on vegetation and vegetation dynamics (Liu *et al.*, 2023), but also appears to reverse historical effects of legacy grazing. A mix of browsers and grazers results in pressure on both grass and shrub species, leading to greater grass cover, more litter, and less compaction (Table S2). While trampling does occur, heterogenous hoof shape - particularly in the Megafauna areas - and the presence of species which can push organic matter into the soil profile is probably partly responsible for the decrease in bulk densities in these areas (Malongweni and Van Tol, 2022).

Finally, the higher frequencies of dung beetles in the Klein Karoo Megafauna area might also contribute to lower bulk densities. As ecosystem engineers, dung beetles churn and transfer above ground organic matter into the soil profile. This process, known as bioturbation, enhances soil aeration and water infiltration, reducing compaction over time. Additionally, the decomposition of buried dung enriches the soil with nutrients, further improving soil structure and fertility (Ma *et al.*, 2023; Torabian, Leffler and Perkins, 2024).

Both vegetation types also experienced a significant change in pH when comparing the Megafauna areas with the Livestock. While the relationships were opposite in nature, both resulted in a shift towards a more neutral pH (towards 7.00). This is likely because lower bulk densities of the Megafauna areas result in easier water infiltration as well as greater movement of nutrient cations and anions (Rodrigues *et al.*, 2024; Ushari, Roopashree and Dhananjay, 2019). In addition, differences in vegetation dynamics (Table S2) result in greater plant cover, more litter, and increased root presence in the Megafauna areas, all of which have a regulatory effect on soil pH (Martins *et al.*, 2021; Staszel-Szlachta *et al.*, 2024). Lastly, with an increase in nutrient cycling (see ammonium, see graph x) and dung beetle abundance in Megafauna areas, it is possible that Megafauna areas experience an increase in microbial activity (Malongweni and Van Tol, 2022; Liu *et al.*, 2023) and have more homogenous soils due to dung beetle movement between horizons (Ma *et al.*, 2023; Torabian, Leffler and Perkins, 2024).

Ammonium levels and the amount of bare ground are significantly higher in the Klein Karoo Megafauna area when compared to the Livestock. These ammonium levels can be explained by higher levels of nutrient cycling because of Megafauna waste excretion and differences in microbial activity (Malongweni and Van Tol, 2022; Liu *et al.*, 2023). In contrast, the higher bare ground percentage can be attributed to the high shrub percentage, as leafy shrub cover results in shading and loss of ground cover (Aslan *et al.*, 2022).

The results of this study imply that the rewilding process has affected soil health since Megafauna reintroduction. While the effects are not identical across vegetation types, overlap is considerable, and the parameters indicate a general positive trend in soil health. In reference to the stated aims and hypotheses, it is clear that Megafauna areas have lower bulk density levels, and pH levels tend more towards neutral levels. Assuming that ammonium levels are indicative of higher nitrogen inputs into the soil, possibly via deposition of waste, results suggest that nutrient cycling in the Megafauna areas is improved when compared to other treatments. However, none of the other metrics support this (Table S2). For example, there were no significant differences seen in organic matter, active carbon or nitrate levels. It is widely recognised that it can take many decades for SOC to respond to changes in management and it is possible that 20 years of rewilding at Sanbona is too short a time to see an effect on SOC stocks.

4.3: Dung Beetles

While it was not possible to run an effective analysis on the abundance of dung beetles in the Renosterveld vegetation type, inferences can be made from the mean values in Table S2. The trend observed in the Klein Karoo indicates that both the Megafauna and Mesoherbivores treatments have significantly higher dung beetle abundance than the Livestock area, which mirrors the observations of Pryke (Pryke, Roets and Samways, 2016, 2022). Further, the Megafauna treatment in both the Klein Karoo and the Renosterveld exhibits the highest dung beetle abundance of all three treatment areas for their respective vegetation types (Table S2). These results suggest that the presence of Megafauna has had a positive impact on dung beetle populations through the creation of a more suitable habitat for dung beetles and a greater abundance of food brought about by changes in vegetation composition as well as dung availability and variety (Schweiger and Svenning, 2018; Torabian, Leffler and Perkins, 2024).

Finally, it is likely that the low number of dung beetles found throughout the Renosterveld is due, at least in part, to less favourable habitat (Sun *et al.*, 2023). Despite these lower numbers compared to the Klein Karoo, the data suggest that rewilding has had a favourable impact on dung beetle numbers in both vegetation types, supporting the stated hypothesis. Further, the comparatively low dung beetle numbers found across both Livestock treatments may be as a result of pesticide and/or anthelmintic use in these areas (Manning, Beynon and Lewis, 2017).

4.4: Vegetation

The impact of rewilding on vegetation communities differs between vegetation types. This is consistent with the literature, as the environmental variables - rainfall, elevation and soil type - differ significantly between Klein Karoo and Renosterveld (Rahmanian *et al.*, 2019; Malongweni and Van Tol, 2022; Liu *et al.*, 2023; Rodrigues *et al.*, 2024).

In the Klein Karoo, shrub cover is significantly higher in the Megafauna area than in the Livestock. These are indigenous trees and shrubs and it is likely that their proliferation is supported by Megafauna feeding habits causing seed dispersal and weed suppression (Shiponeni and Milton, 2006; Kalbitzer *et al.*, 2019). Further, the impact of Megafauna on soil health through nutrient cycling conceivably further encourages tree and shrub growth in the area. In contrast, the lack of shrubs seen in the Livestock area is likely partly due to historically unfavourable livestock and agricultural practices, resulting in the deterioration of soil health (Rahmanian *et al.*, 2019).

Succulent numbers, on the other hand, are far greater in Livestock than in both the Megafauna and Mesoherbivores areas. This corresponds with the literature on the Megafauna area, as analysis of dietary preferences show that elephants in these areas favour succulents (Vorster, Hoffman and Todd, 2017; Swanepoel and Alison, 2019; Liesl Vorster, 2024, pers.comm). It is possible that non-livestock ungulates also feed on succulents. It is also worth noting that the Livestock area in the Klein Karoo is currently undergoing a resting period, and it is therefore possible that the lack of grazing pressure has allowed succulent numbers to increase.

In contrast, shrub cover in the Renosterveld is highest in the Mesoherbivores area, followed by the control (livestock) and lowest in the Megafauna area. A crucial distinction here is that the shrub cover in the Livestock area is dominated by an invasive weed (Liesl Vorster, 2024, pers. comm) and not indigenous tree or shrub species as found in the Megafauna and Mesoherbivores areas. While management in the Livestock area has recently implemented a regenerative grazing approach, the impact of such changes is yet to be seen in this regard.

Elevation was seen to have a strong influence on shrub cover in the Renosterveld and is likely a contributing factor, as is rainfall. However, dietary analysis of the Renosterveld herd (Vorster, Hoffman and Todd, 2017; Swanepoel and Alison, 2019) shows a strong preference for shrub and tree species. As such, it is likely that browsing habits of Megafauna are impacting the shrub cover in this area, a phenomenon further supported by the fact that the Mesoherbivores area contains the highest shrub cover of all three treatments. It’s likely that the lack of browsing pressure by Megafauna is not having a detrimental impact on shrub cover in this treatment area. However, all conclusions drawn are tentative at best, owing to numerous variables that can not be controlled.

When considering litter, however, the inverse relationship is true. The Megafauna area has the highest litter cover at roughly 40%. It is possible, therefore, that movement of Megafauna causes broken branches to fall to the ground and the trampling of grasses (Swanepoel and Alison, 2019; Gordon *et al.*, 2023). This is partially supported by the fact that organic matter values in the Megafauna area are the highest of any treatment in the Renosterveld vegetation type (Table S2), which matches previous findings reported in the literature as referenced above.

EVI results in the Klein Karoo suggest that the presence of Megafauna drastically impacts vegetation cover, both positively and negatively, depending on environmental condition. In good rainfall areas, the presence of Megafauna seems to have a magnifying effect, as EVI readings are much higher than those of the other treatment areas. In contrast, in drought years, the EVI scores in the Megafauna area decrease sharply. This is likely due to reduced carrying capacity during these drought periods with no reduction in stocking rates (Rahmanian *et al.*, 2019; Wells *et al.*, 2022). Historically, Megafauna were able to move across landscapes during times of drought in search of better vegetation (Tshipa *et al.*, 2017; Black *et al.*, 2024). However, with the closed systems so prevalent in the Anthropocene, the ability to migrate no longer exists. This is potentially a strong argument for the establishment of green migration corridors in the future. Ultimately, the trends are similar across treatments, and it is the degree to which the trends are magnified that is so demonstrably influenced by Megafauna presence. The EVI scores in the Mesoherbivores area are also substantially higher than those of the control (livestock) area. This suggests that the presence of indigenous ungulates who evolved concurrently with the local vegetation positively impacts vegetation by promoting healthy growth and diverse ecosystems. It also suggests that outdated Livestock practices negatively impact vegetation (Rahmanian *et al.*, 2019).

In the Renosterveld, EVI scores revealed that differences between treatments are far less pronounced. Nonetheless, there is a substantial decrease in EVI in the Megafauna area during the 2015-2016 drought that is not seen in the other treatment areas. The recovery period after this drought is also substantial, with the EVI scores only rebounding after 10 years, which supports the notion that carrying capacity during this time may have been too high, highlighting the importance of migration and the subsequent need for green migration corridors (Tshipa *et al.*, 2017; Rahmanian *et al.*, 2019; Black *et al.*, 2024).

4.5: Soil organic carbon stocks and credits

Soil organic carbon stocks for the Klein Karoo Megafauna area was the lowest of all treatments for that vegetation type. This could be explained by the relatively lower bulk densities experienced in this area, as well as potential differences in microbial community differences, though this was not tested. Since bulk density is an important factor in calculating soil carbon, it is likely that a reduced bulk density reduces the carbon stock due to the concentration being expressed on a per volume basis. However, the Megafauna area in the Renosterveld showed the highest SOC levels and while analysis (Table S1) showed that there were no significant differences in organic carbon between treatments, these differences should still be noted.

Both Megafauna areas had relatively higher EVI and shrubs, much of this aboveground biomass may not necessarily result in increased SOC stock or it may take a longer time to do so. Arid areas will certainly have relatively slower decomposition rates when compared to mesic areas. Together, these findings suggest that carbon credits are not necessarily a viable funding method for semi-arid areas such as these if only soil carbon is considered, however, it may be more of a viable option for renosterveld than Klein Karoo. Evidence suggests, however, that a shift to biodiversity credits, and a more holistic measurement of ecosystem health, may be beneficial and serve as a funding tool in these circumstances.

4.6: Limitations and recommendations

Further similar studies should be conducted over an extended period, spanning several years and over different seasons, to understand both long term effects and changes, and seasonal shifts and differences. Furthermore, it is advisable to use various capture methods for the dung beetle collection, such as light traps, to potentially attract a larger variety of dung beetle species and thus attain a more comprehensive understanding about their abundance and community dynamics. There is also a need for a long-term comprehensive vegetation community study, to explore potential changes in species composition as the rewilding process, and its effects, develop over time. In addition, fire is an important part of these systems, particularly in Renosterveld, and is considered a valuable management tool. However, its impact has not been considered or mentioned due to lack of reliable record keeping and study constraints. That said, further studies should include fire as a variable, where appropriate, particularly when considering soil factors such as nutrients. Another limitation is the comparison across spatially separated treatments, which may be influenced by unmeasured confounding factors such as subtle edaphic or historical differences. This limits the ability to draw strong causal inferences, and results should therefore be interpreted with caution. Lastly, these data would also benefit from the additional inclusion of microbial community analysis, to understand how the presence of terrestrial fauna impacts subterranean micro fauna communities and ultimately, soil health at a biological level.

4.7: Conclusions

The impact of rewilded megafauna differs significantly between the Renosterveld and Klein Karoo vegetation types, and is shaped by co-varying factors such as elevation, soil type, rainfall, geology, and plant community composition. In the Klein Karoo, the impact of megaherbivore rewilding was pronounced, with direct effects observed at the level of individual plants, plant communities, soils, and invertebrates. In contrast, the impact of megafauna in the Renosterveld was less notable, with observable changes limited primarily to soil characteristics.

Although active carbon levels (Table S1) did not vary significantly between treatments within either vegetation type—even when the impact of megafauna on ecosystem health was statistically evident—they did differ significantly between the two vegetation types. This demonstrates a key shortcoming of using carbon levels as a standalone measure of ecosystem health and rehabilitation success. A more nuanced and context-sensitive approach is necessary when evaluating ecosystem impact and determining appropriate mechanisms for recognising and rewarding responsible land stewardship.

Rewilding and its effects are highly layered and complex. While whole, intact ecosystems tend to be the most stable and resilient to adverse change, the influence of ecosystem engineers—including megafauna—is strongly dependent on the abiotic environmental context. The composition of the ecological community, along with the interaction between biotic and abiotic factors, plays a major role in determining the nature and magnitude of the impact following the reintroduction of such species.

For this reason, the approach taken in this study was deliberately holistic, aiming to understand the impact of megafauna reintroduction in the Sanbona area by examining soil characteristics (both physical and chemical), vegetation community composition, and invertebrate (dung beetle) abundance. This analysis also accounted for variation between vegetation types and, where possible, considered co-variables such as elevation and soil texture.

Ultimately, the way in which ecosystem engineers influence their environment after reintroduction evolves over time, shaped by both changing conditions and a mix of direct and indirect effects. In this study, these temporal and spatial dynamics were explored at the vegetation level using Enhanced Vegetation Index (EVI) data, comparing current vegetation cover across different land use types (Megafauna, Mesoherbivores, and Livestock) to satellite imagery from two decades ago.

The findings from this study suggest that rewilding, through megafauna reintroduction, has the potential to enhance ecosystem function, as indicated by improvements in soil properties, vegetation dynamics, and dung beetle abundance in rewilded areas. However, many of these findings remain tentative and are at least partially influenced by other environmental factors. As such, the trends observed should be interpreted with caution, given the complexity and variability of the systems and data involved. While the results are promising, they also highlight the need for more in-depth, long-term research.

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SUPPLEMENTARY MATERIALS

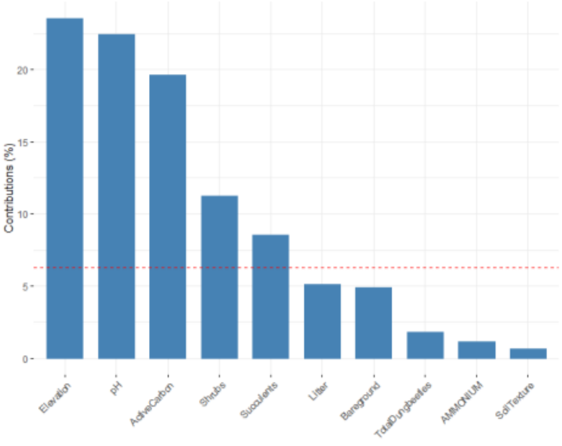

Figure 1. Contribution of variables to Dim-1

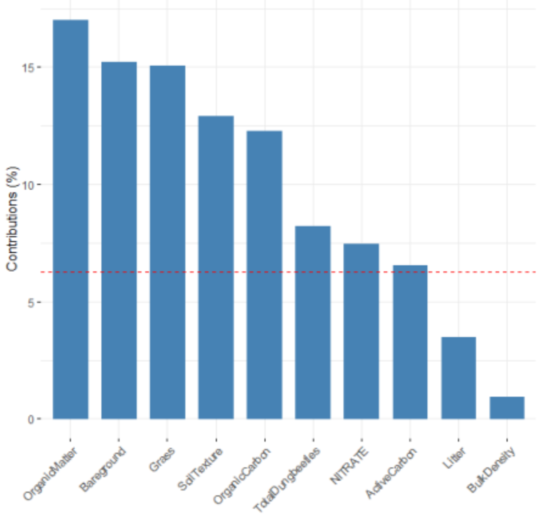

Figure 2. Contribution of variables to Dim-2

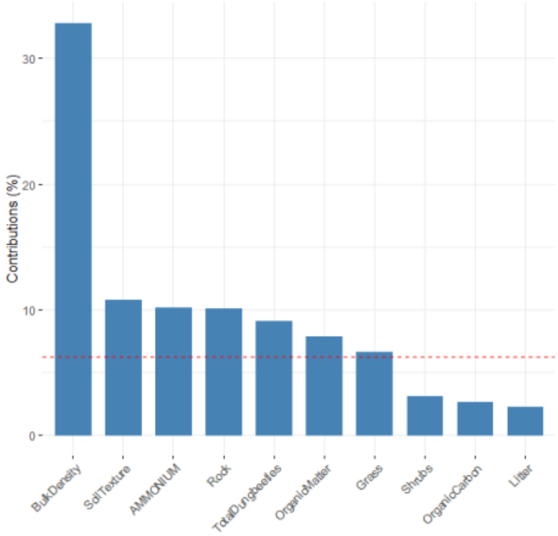

Figure 3. Contribution of variables to Dim-3

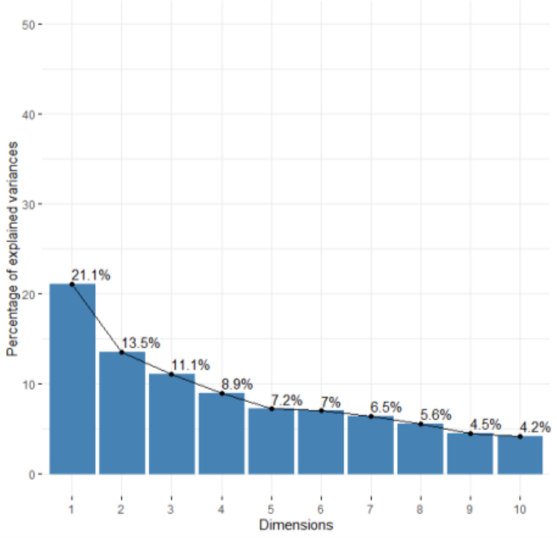

Figure 4. Scree plot

Figure 11. Contribution graphs for dimensions 1, 2 and 3, showing the most relevant variables, in addition to a Scree plot.

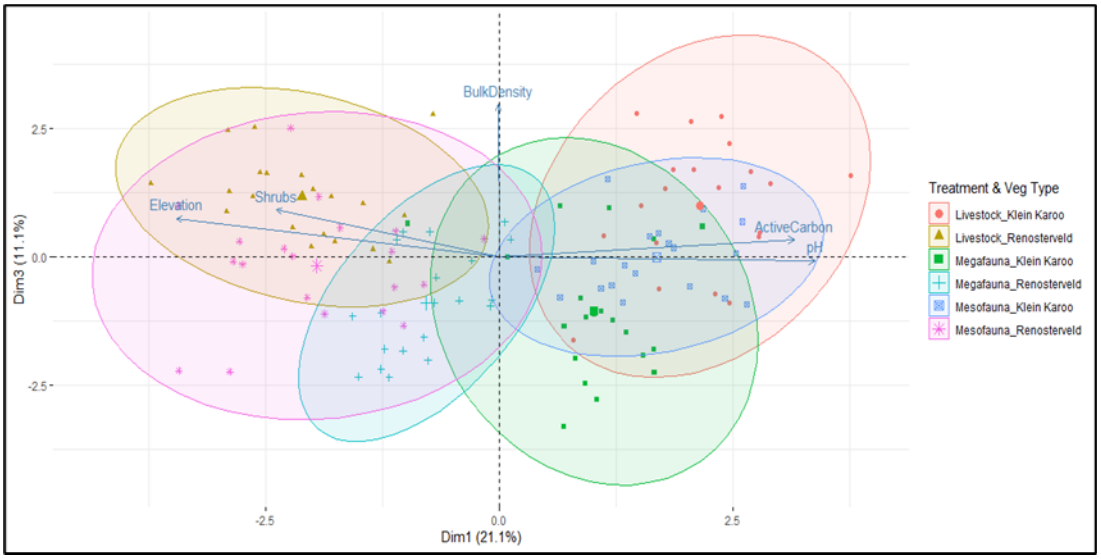

Figure 12. PCA of all variables (Dim1 vs Dim3).

Figure 13: Example of methods used to collect grid vegetation variables and (left) dung beetle traps (right).

Figure 14: *Scarabeus viator,* the most common dung beetle species collected in this study.

Table S1: Pairwise Analysis summaries.

Model	Contrast	Estimate	SE	P value
AMMONIUM_KK	Livestock - Megafauna	-0.304	0.112	0.024
AMMONIUM_KK	Livestock - Mesofauna	-0.173	0.112	0.277
AMMONIUM_KK	Megafauna - Mesofauna	0.131	0.112	0.478
AMMONIUM_RV	Livestock - Megafauna	-0.168	0.113	0.305
AMMONIUM_RV	Livestock - Mesofauna	-0.091	0.113	0.701
AMMONIUM_RV	Megafauna - Mesofauna	0.077	0.113	0.775
NITRATE_KK	Livestock - Megafauna	-0.735	2.083	0.934
NITRATE_KK	Livestock - Mesofauna	3.024	3.140	0.603
NITRATE_KK	Megafauna - Mesofauna	3.759	2.797	0.377
NITRATE_RV	Livestock - Megafauna	0.962	1.960	0.876
NITRATE_RV	Livestock - Mesofauna	1.526	1.960	0.718

NITRATE_RV	Megafauna - Mesofauna	0.564	1.960	0.955
ORGCARBON_KK	Livestock - Megafauna	0.075	0.087	0.660
ORGCARBON_KK	Livestock - Mesofauna	0.091	0.087	0.548
ORGCARBON_KK	Megafauna - Mesofauna	0.016	0.087	0.982
ORGCARBON_RV	Livestock - Megafauna	-1.874	2.438	0.724
ORGCARBON_RV	Livestock - Mesofauna	-0.041	0.195	0.975
ORGCARBON_RV	Megafauna - Mesofauna	1.833	2.374	0.722
ORGMATTER_KK	Livestock - Megafauna	0.250	0.257	0.597
ORGMATTER_KK	Livestock - Mesofauna	0.984	1.233	0.706
ORGMATTER_KK	Megafauna - Mesofauna	0.734	1.171	0.806
ORGMATTER_RV	Livestock - Megafauna	0.256	0.174	0.312
ORGMATTER_RV	Livestock - Mesofauna	0.259	0.174	0.303
ORGMATTER_RV	Megafauna - Mesofauna	0.004	0.174	1.000
ACTIVECARBON_KK	Livestock - Megafauna	74.065	32.605	0.068
ACTIVECARBON_KK	Livestock - Mesofauna	192.260	102.550	0.156
ACTIVECARBON_KK	Megafauna - Mesofauna	118.195	89.483	0.390
ACTIVECARBON_RV	Livestock - Megafauna	-53.722	46.271	0.482
ACTIVECARBON_RV	Livestock - Mesofauna	-2.438	46.271	0.998
ACTIVECARBON_RV	Megafauna - Mesofauna	51.284	46.271	0.514
BULKDENSITY_KK	Livestock - Megafauna	0.170	0.000	0.000
BULKDENSITY_KK	Livestock - Mesofauna	0.129	0.000	0.000

BULKDENSITY_KK	Megafauna - Mesofauna	-0.041	0.000	0.000
BULKDENSITY_RV	Livestock - Megafauna	0.184	0.037	0.000
BULKDENSITY_RV	Livestock - Mesofauna	0.234	0.037	0.000
BULKDENSITY_RV	Megafauna - Mesofauna	0.050	0.037	0.368
PH_KK	Livestock - Megafauna	0.852	0.081	0.000
PH_KK	Livestock - Mesofauna	1.131	0.517	0.084
PH_KK	Megafauna - Mesofauna	0.279	0.503	0.845
PH_RV	Livestock - Megafauna	-0.555	0.074	0.000
PH_RV	Livestock - Mesofauna	-0.295	0.074	0.001
PH_RV	Megafauna - Mesofauna	0.260	0.074	0.003
TOTALDUNGBEETLES_KK	Livestock - Megafauna	-3.619	1.145	0.007
TOTALDUNGBEETLES_KK	Livestock - Mesofauna	-10.909	3.502	0.008
TOTALDUNGBEETLES_KK	Megafauna - Mesofauna	-7.289	3.103	0.058
BAREGROUND_KK	Livestock - Megafauna	-0.664	0.346	0.143
BAREGROUND_KK	Livestock - Mesofauna	-0.994	0.347	0.016
BAREGROUND_KK	Megafauna - Mesofauna	-0.330	0.347	0.610
BAREGROUND_RV	Livestock - Megafauna	-0.666	0.789	0.678
BAREGROUND_RV	Livestock - Mesofauna	-0.139	0.786	0.983
BAREGROUND_RV	Megafauna - Mesofauna	0.528	0.788	0.782

LITTER_KK	Livestock - Megafauna	1.150	0.498	0.064
LITTER_KK	Livestock - Mesofauna	0.886	0.494	0.183
LITTER_KK	Megafauna - Mesofauna	-0.264	0.507	0.862
LITTER_RV	Livestock - Megafauna	-0.927	0.321	0.015
LITTER_RV	Livestock - Mesofauna	-0.186	0.328	0.838
LITTER_RV	Megafauna - Mesofauna	0.741	0.318	0.061
GRASS_KK	Livestock - Megafauna	-0.721	0.570	0.420
GRASS_KK	Livestock - Mesofauna	-3.769	2.137	0.192
GRASS_KK	Megafauna - Mesofauna	-3.048	1.952	0.271
GRASS_RV	Livestock - Megafauna	-1.648	0.774	0.095
GRASS_RV	Livestock - Mesofauna	-1.676	0.750	0.076
GRASS_RV	Megafauna - Mesofauna	-0.028	0.768	0.999
SHRUBS_KK	Livestock - Megafauna	-2.304	0.518	0.000
SHRUBS_KK	Livestock - Mesofauna	-1.949	0.839	0.062
SHRUBS_KK	Megafauna - Mesofauna	0.354	0.741	0.882
SHRUBS_RV	Livestock - Megafauna	1.338	0.580	0.064
SHRUBS_RV	Livestock - Mesofauna	-0.428	0.576	0.739
SHRUBS_RV	Megafauna - Mesofauna	-1.767	0.579	0.010
SUCCULENTS_KK	Livestock - Megafauna	0.836	0.455	0.167
SUCCULENTS_KK	Livestock - Mesofauna	1.153	0.453	0.036
SUCCULENTS_KK	Megafauna - Mesofauna	0.317	0.445	0.758

SUCCULENTS_RV	Livestock - Megafauna	-0.280	0.321	0.660
SUCCULENTS_RV	Livestock - Mesofauna	0.000	0.317	1.000

Table S2: Mean and standard deviation (SD) of all variables from this study.

Vegetation Type	Treatment	Variable	Mean	SD
Klein Karoo	Livestock	Elevation	435.400	6.411
	Livestock	Total dung beetles	0.650	0.988
	Livestock	AMMONIUM	0.405	0.266
	Livestock	NITRATE	10.179	7.204
	Livestock	Organic Carbon	0.568	0.304
	Livestock	Active Carbon	811.715	63.260
	Livestock	Organic Matter	0.926	0.436
	Livestock	Clay	0.421	0.065
	Livestock	Silt	16.614	2.561
	Livestock	Sand	82.965	2.619
	Livestock	Bulk Density	1.521	0.093
	Livestock	pH	7.518	0.157
	Livestock	Bare ground	39.150	22.151
	Livestock	Rock	17.500	22.258
	Livestock	Litter	15.150	10.898
	Livestock	Grass	3.350	12.729
	Livestock	Shrubs	1.450	2.605
	Livestock	Succulents	23.400	25.363
	Megafauna	Elevation	429.200	13.017
	Megafauna	Total dung beetles	2.400	3.899
	Megafauna	AMMONIUM	0.709	0.414
	Megafauna	NITRATE	11.441	6.974
	Megafauna	Organic Carbon	0.492	0.279
	Megafauna	Active Carbon	779.329	91.630
	Megafauna	Organic Matter	1.060	0.526
	Megafauna	Clay	0.672	0.657
	Megafauna	Silt	19.678	16.904
	Megafauna	Sand	79.650	17.553
	Megafauna	Bulk Density	1.358	0.066
	Megafauna	pH	6.763	0.202

	Megafauna	Bare ground	57.900	31.782
	Megafauna	Rock	0.400	0.995
	Megafauna	Litter	6.200	6.971
	Megafauna	Grass	18.150	30.325
	Megafauna	Shrubs	14.300	19.181
	Megafauna	Succulents	3.550	5.424
	Mesoherbivores	Elevation	403.800	2.191
	Mesoherbivores	Total dung beetles	0.900	1.889
	Mesoherbivores	AMMONIUM	0.578	0.365
	Mesoherbivores	NITRATE	9.802	5.058
	Mesoherbivores	Organic Carbon	0.477	0.232
	Mesoherbivores	ActiveCarbon	785.928	67.504
	Mesoherbivores	OrganicMatter	0.952	0.488
	Mesoherbivores	Clay	0.241	0.215
	Mesoherbivores	Silt	11.104	7.445
	Mesoherbivores	Sand	88.655	7.640
	Mesoherbivores	BulkDensity	1.423	0.068
	Mesoherbivores	pH	7.143	0.073
	Mesoherbivores	Bareground	66.100	18.990
	Mesoherbivores	Rock	1.250	3.697
	Mesoherbivores	Litter	9.750	10.197
	Mesoherbivores	Grass	4.950	9.327
	Mesoherbivores	Shrubs	8.600	12.717
	Mesoherbivores	Succulents	9.350	17.361
Renosterveld	Livestock	Elevation	720.200	5.001
	Livestock	Total dung beetles	0.000	0.000
	Livestock	AMMONIUM	0.597	0.355
	Livestock	NITRATE	10.801	5.667
	Livestock	OrganicCarbon	0.469	0.269
	Livestock	ActiveCarbon	615.955	91.944
	Livestock	OrganicMatter	1.156	0.572
	Livestock	Clay	0.794	0.425
	Livestock	Silt	12.721	5.017
	Livestock	Sand	86.484	5.406
	Livestock	BulkDensity	1.564	0.069
	Livestock	pH	5.927	0.164
	Livestock	Bareground	42.300	28.208
	Livestock	Rock	4.050	6.436
	Livestock	Litter	21.150	19.362

	Livestock	Grass	1.950	3.252
	Livestock	Shrubs	30.550	30.531
	Livestock	Succulents	0.000	0.000
	Megafauna	Elevation	541.800	2.628
	Megafauna	Total dung beetles	0.850	1.040
	Megafauna	AMMONIUM	0.765	0.363
	Megafauna	NITRATE	9.839	6.851
	Megafauna	OrganicCarbon	0.570	0.331
	Megafauna	ActiveCarbon	669.677	90.771
	Megafauna	OrganicMatter	0.900	0.407
	Megafauna	Clay	0.636	0.126
	Megafauna	Silt	21.621	4.892
	Megafauna	Sand	77.743	4.999
	Megafauna	BulkDensity	1.380	0.121
	Megafauna	pH	6.481	0.204
	Megafauna	Bareground	36.900	19.079
	Megafauna	Rock	0.150	0.671
	Megafauna	Litter	40.700	21.551
	Megafauna	Grass	9.650	9.161
	Megafauna	Shrubs	11.550	10.640
	Megafauna	Succulents	1.050	2.724
	Mesoherbivores	Elevation	702.000	7.595
	Mesoherbivores	Total dung beetles	0.150	0.489
	Mesoherbivores	AMMONIUM	0.688	0.354
	Mesoherbivores	NITRATE	9.275	6.017
	Mesoherbivores	OrganicCarbon	0.524	0.391
	Mesoherbivores	ActiveCarbon	618.393	96.445
	Mesoherbivores	OrganicMatter	0.897	0.462
	Mesoherbivores	Clay	0.739	0.169
	Mesoherbivores	Silt	16.157	5.166
	Mesoherbivores	Sand	83.103	5.318
	Mesoherbivores	BulkDensity	1.330	0.145
	Mesoherbivores	pH	6.221	0.311
	Mesoherbivores	Bareground	25.250	20.274
	Mesoherbivores	Rock	10.600	16.214
	Mesoherbivores	Litter	23.550	20.469
	Mesoherbivores	Grass	11.950	15.371
	Mesoherbivores	Shrubs	28.650	17.015
	Mesoherbivores	Succulents	0.000	0.000

Table S3: Dung beetle species collected in this study.

Species	**Number**
Scarabeus viator	55
Gymnopleurus humanus	1
Euoniticellus triangulatus	2
Onthophagus peringueyi	2
Sisyphus quadricollis	4
Cheironitis scabrosus	13
Onthophagus sp. Group 16	8
Scarabaeus satyrus	13
Scarabaeus proboscideus	1